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Early Development of the Clingfish, *Gobiesox strumosus* Cope[1]

SUZANNE RUNYAN

ABSTRACT

Descriptions and illustrations of the egg, early larval stages, and young of the clingfish, *Gobiesox strumosus*, are presented for the first time. The eggs and early larvae are compared briefly with those of ecologically similar species. Morphometric and meristic data are also provided for 95 specimens ranging from 2.85 to 50 mm total length (T.L.). Skeletal drawings of stained and cleared specimens show progression of ossification.

The eggs of the clingfish are laid in empty oyster shells and are distinguished from other ecologically similar species in upper Chesapeake Bay area by their ovate shape. The egg number per cluster ranges from about 300 to 2500. A single cluster may contain eggs in several different developmental stages. The diagnostic feature of the pre-hatching embryo is lack of pigment on the yolk and head and heavy pigmentation on the trunk. Eggs hatch within five to seven days. Chances of survival are much greater for eggs tended by an adult fish throughout the incubation period.

The average hatching length of larvae is between 3.4–3.8 mm T.L. with yolk already absorbed, but artificial conditions may cause the embryo to hatch between 2.8–3.4 mm with yolk still present. Diagnostic features include a broad head and laterally compressed body with spatulate tail; large, heavily-pigmented eyes; 10–15 stellate melanophore saddles; and the absence of pigment on the posterior 30 per cent of the body.

By 12 mm T.L. the young clingfish is essentially similar to the adult in appearance, although some osseous structures are still incomplete and pigmentation has not yet developed into the definitive reticulated patterns of the adult. By 40 mm T.L. the clingfish can properly be considered an adult.

When measured against standard length, the dependent variables of head length, snout-to-anus length, eye length, disc length, and greatest body depth are seen to be proportional in their rate of growth. The head increases while the eye decreases, relative to body growth.

Introduction

The objective of this study is to describe the life history of the clingfish, *Gobiesox strumosus* Cope, especially its early development. This is accomplished by (1) providing qualitative information in illustrations and descriptions of the eggs, young, and adults, (2) presenting quantitative summaries in the form of meristic and morphometric data, and (3) pointing out briefly the characteristic features of the early development that distinguish it from ecologically similar species with which it is found. These observations were made on a Chesapeake Bay population from the Patuxent River at Solomons, Maryland.

There has been relatively little information recorded concerning this small species, commonly known as the clingfish, oysterfish,

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and more recently skilletfish. Existing literature emphasizes the descriptive, morphometric, and meristic features of the adult clingfish (Jordan and Evermann, 1898: 2333; Hildebrand and Schroeder, 1928: 339–40; Longley and Hildebrand, 1941: 283–5; Pearson, 1941:99–100; Schultz, 1944:65–8; and Briggs, 1955:115–7). On the other hand, studies on the embryology, the larval forms, and the early development stages of *Gobiesox strumosus* are scarce. Pearson is the only author who has identified the larvae and young. Furthermore, illustrations of eggs, larvae, and young are lacking in the literature.

Gobiesox strumosus is an estuarine and marine species distributed from Santos, Sao Paulo, Brazil, to New Jersey, including the West Indies, Gulf of Mexico, and Bermuda (Hildebrand and Schroeder, 1928:340; Longley and Hildebrand, 1941:285; and Briggs, 1955:116). It is adapted to a rather sedentary life and is remarkable for the development of a ventral, adhesive disc used for attachment to relatively stable objects such as oyster shells, pilings, rocks, and loggerhead sponges. Therefore, even in localities where it is abundant, it is not often seined, trapped, or brought up in nets. Pearson (1941:100) observed that no fish over 45 mm in length were obtained in the plankton. On the other hand, it is easily obtained in experimental oyster trays and other open containers left on the bottom. It is usually taken in shallow, brackish waters and particularly around oyster bars. Although it is too small to have any economic value, it might be a vector or reservoir for oyster parasites; in which case, a greater knowledge of its life cycle and habits could have great importance. Also, it may be of some bionomic significance because of the habit of laying its eggs in empty oyster shells, thereby causing the shells to remain in cleaner condition for the subsequent seeding of young oysters.

Acknowledgments:—The author gratefully acknowledges the extensive assistance given by Dr. Romeo J. Mansueti, Senior Fisheries Biologist, Chesapeake Biological Laboratory, in his supervision and editing of this paper and to his wife, Alice Jane Mansueti, medical illustrator, for advice in the production of illustrations. I also wish to extend my sincere appreciation to Mrs. Ranice W. Davis, Director of the Department of Art as Applied to Medicine, at the Johns Hopkins University School of Medicine, for her help and advice in the preparation of this manuscript, particularly with reference to the illustrations. My thanks go to Mr. William Dovel of the Chesapeake Biological Laboratory for helping me to obtain clingfish eggs and specimens, and to the whole staff of the Chesapeake Biological Laboratory for the use of their facilities while doing my research.

Methods and Materials

All specimens of *Gobiesox strumosus* were collected at Solomons in the vicinity of the pier of the Chesapeake Biological Laboratory, which extends nearly 740 feet out into the mouth of the Patuxent River in a southeasterly direction. The depth of the water at the end of the pier is about eight feet at mean low tide. Tidal currents in this area are rather weak.

Solomons, Calvert County, Maryland, is situated partly on a small island within the mouth of the Patuxent River, about 1¾ miles from the point where this broad estuary empties into Chesapeake Bay. The river bottom in this area is fairly even in its slope, reaching a depth of 50–60 feet in its main channel. The bottom is sandy and relatively barren except for several oyster bars and scattered stands of eelgrass, *Zostera marina*. Valuable fisheries for oysters, clams, crabs, and finfish are supported by the surrounding brackish waters. Although the tidal amplitude increases upstream, its mean is only 1.2 feet at Solomons.

Mean salinity values at Solomons have the following seasonal concentrations: winter—14.8‰; spring—11.4; summer—12.3; and fall—15.7‰. Mean, surface water temperatures are as follows: winter—4.3° C, spring—11.9° C, summer—25.6° C, fall—18.2° C. The average daily range is 1.2° with a maximum daily range of 3.0° occurring several times in late winter and spring and again in early fall. The water tempera-

tures bear quite a close relationship to air temperatures but show less fluctuation (Beaven, 1960:8).

Oyster trays were placed on the bottom in water three to six feet deep to attract and procure specimens. The trays were filled with the empty shells of the oyster, *Crassostrea virginica*, which the fish seemed to prefer over the exterior shells of live oysters. I also acquired a few specimens from nets dragged through eelgrass and plankton at a depth of three feet. In the tray collection the clingfish were invariably associated with the striped blenny, *Chasmodes bosquianus*, the naked goby, *Gobiosoma bosci*, and the seaboard goby, *Gobiosoma ginsburgi*. In the free-swimming collections they were also taken with northern pipefish, *Syngnathus fuscus*, and fourspine sticklebacks, *Apeltes quadracus*. Other species also are occasionally found with them, notably the feather blenny, *Hypsoblennius hentz*, and the green goby, *Microgobius thalassinus*. An important part of this project was devoted to establishing criteria for distinguishing the eggs and larvae of *Gobiesox strumosus* from associated eggs and larvae of gobies and blennies that also spawn in oyster shells. Except for a few fish which were kept alive for spawning purposes, these specimens were preserved in five per cent formalin for measurement and illustration at a later date.

The problem of studying the embryology of *Gobiesox strumosus* lay in the difficulty of obtaining eggs that were indisputedly clingfish eggs and not those belonging to gobies and blennies, particularly since they had not yet been identified and described in the literature. Masses of roundish, yellow eggs laid in empty shells had been found in the oyster trays on many occasions. As clingfish were seen with these eggs and sometimes even occupying the same shell, it was presumed that these were the eggs of *G. strumosus*. However, since the ecologically-related blennies and gobies were also found among the same shells, they might just as easily have been the source of these eggs, as the latter on superficial examination are quite similar in appearance.

The method of stripping eggs from ripe female clingfish and fertilizing them with milt from male clingfish was discarded because enough ripe fish could not be easily procured and also because the process seemed rather unpredictable, especially since there seems to be no obvious external sexual dimorphism. Therefore, in order to *prove* the identity of clingfish eggs, a floating box was populated only with adult *Gobiesox strumosus*, which laid and fertilized their own eggs. This project was carried out during the last two weeks of June, 1960. In fall 1960, young and adults were collected at Solomons, and specimens were stained and cleared at the laboratory. Further work on eggs and larvae, with emphasis on hatching, was also carried out in spring 1961, at Solomons.

The box was constructed of wood and plastic screening. Opposite sides of the box had windows of plastic screening for a continuous flow of water. A lid of screening was also provided to prevent loss of specimens if the box were accidentally submerged because of stormy weather. The box was supplied with about four inches of clean oyster shells, which had first been thoroughly washed to insure that they were free from eggs of any kind. Then, on the assumption that among a dozen fish both sexes would be represented, 12 adult clingfish were put in the box which was tied to the pier in water three feet deep.

Eggs were obtained by checking the shell surfaces in the floating box each morning. Once the eggs were identified, the box was no longer necessary; and eggs were taken directly from the oyster trays. Unpublished descriptions and illustrations of eggs hatched in the Laboratory from clingfish isolated in the same manner as described above by Mansueti (1956A:134–43) showed them to be identical to the author's eggs. The larvae reared by him at the time were compared to a group of 56–60 larvae taken near the pier on June 23, 1960. After prolonged observation, the two collections were seen to be identical; thus, the latter were positively identified as *Gobiesox strumosus*. Further confirmation of this decision was given by actually hatching the eggs of *G. strumosus* in May, 1961, and by comparing

the larvae with other species of gobies and blennies; those classified as *Gobiesox* were singularly different. Both eggs and larvae were preserved in formalin and used later for measurements.

In making measurements of the eggs, larvae, and young of *Gobiesox strumosus* a stereoscopic microscope with a micrometer ocular was used. Calibration was necessary to translate the magnification of various lenses into millimeters.

Except when dealing with physical characteristics peculiar to the clingfish (i.e., the adhesive disc), the standard for measurements and meristic counts was derived from Hubbs and Lagler (1947:8–15). Definitions for measurements not given by the latter reference are as follows:

(a) length of disc—distance between the outermost edges of the lengthwise flare;
(b) width of disc—distance between the widest parts of the anterior collar, excluding the flared pelvic fins;
(c) chin to disc—distance from tip of chin to anterior base of disc where it joins the body; and
(d) disc to anus—distance from the cartilaginous base of the rear margin of the disc to the anus.

The disc length measurement is similar to that taken by Briggs (1955:4), but (c) is different. Measuring to the base of the disc seemed much more constant than measuring to the edge of the flare; thus, the reason for its use. Measurements (b) and (d) were not made by Briggs.

As noted previously, all measurements were made on preserved specimens. It was thought that shrinkage would be uniform, and, according to Mansueti (1958A:5), such effects are probably negligible in the overall results.

The calculations in the morphometric tables and graphs are based on original measurements of 95 specimens. In the table showing changes in body proportions only standard lengths (distance from the tip of the snout to the tip of the urostyle) were used for the computations, although total lengths (distance from the tip of the snout to the tip of the finfold or caudal fin) are used in the text for purposes of orientation to the actual size of the fish. However, both standard and total lengths are carefully designated as such wherever they are used.

In the morphometric graphs showing regression of body parts the regression lines were fitted by using the method of least squares, based on the straight line formula, $Y = a + bX$, and calculated from averages taken of original measurements in two millimeter intervals. In all cases, standard length was used as the independent variable.

Results and Discussion

Spawning Season and Location:—Recent observations indicate that *Gobiesox strumosus* spawns principally from April through August, with a peak spawning in June and July. Hildebrand and Schroeder (1928:340) apparently erred in the estimate of the length of the spawning season, indicating that it occurs only during April and May. Pearson (1941:82) found larvae and young from May through August in plankton samples taken over oyster bars. Mr. G. F. Beaven, oyster biologist at the Chesapeake Biological Laboratory, believes that it is the first oyster community species to spawn in spring. Dr. Mansueti and Mr. William Dovel, also at the Laboratory, observed eggs of *G. strumosus* to hatch in late July. Spawning is apparently largely restricted to oyster reefs and similar estuarine bottoms. Temperature is an important factor; at least 65° F is necessary for spawning. When spring is early, spawning probably begins in April; but when water temperatures remain low in spring, as they did in 1961, they will not spawn until late in May.

Development of the Egg:—The eggs of *Gobiesox strumosus* are laid in an adhesive mass on the inner concave surfaces of empty oyster shells. The fish sometimes lay them upside down, as shown by the position of undisturbed shells. The eggs adhere firmly to each other in a single layer and to the surface on which they are laid. Because of this sticky mucus which hardens under water and which Ryder (1884:462) says is probably developed as a secretion of the

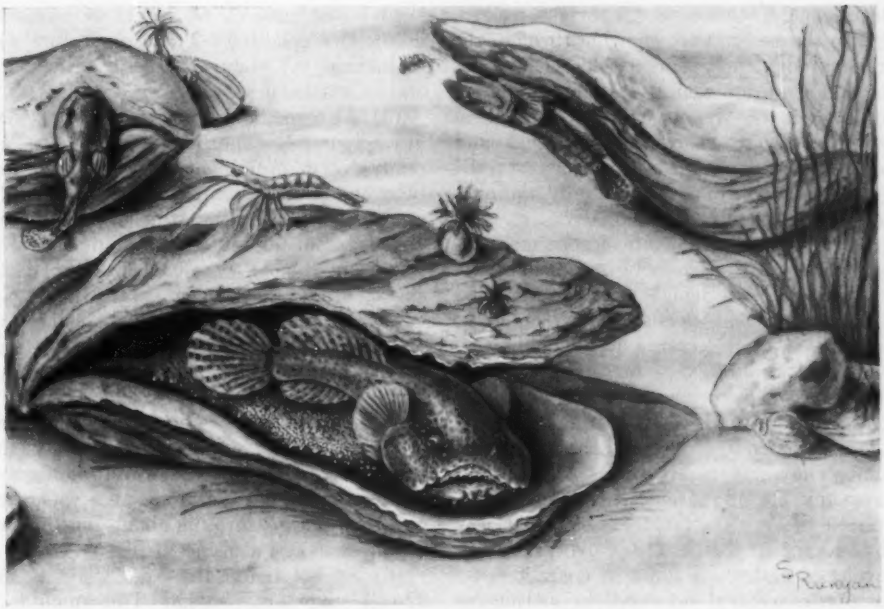


Fig. 1.—Environment among oyster shells of the clingfish, *Gobiesox strumosus*, showing adults in characteristic attitudes. Note also the variations in pigment pattern among the adults.

ovarian follicle, it is quite difficult to pry the eggs off the shell unharmed, even when gently teased apart with a needle.

The egg clusters vary greatly in size, some filling an entire large shell, while others may cover an area no larger than four to six square centimeters. One shell obtained contained approximately 650 eggs distributed over 16 square centimeters in a shell surface measuring about 45 square centimeters in area. In one hinged oyster shell with an inner surface area of approximately 130 square centimeters, both valves were covered with eggs in an area totaling about 86 square centimeters and containing some 2,500 eggs. The average number of eggs per square centimeter seems to be around 30–35.

It is probable that a single female can deposit on successive periods, as suggested below, from 300 to 2,500 eggs. These figures represent the approximate numerical extremes observed on shells. A sexually mature, average-sized female 53 mm T.L. contained a total of 1600 large-yolked eggs (range 0.66–0.76 mm, mean 0.71 mm) just before ovulation. There is also sometimes a variation of developmental stages within a cluster. In the first cluster mentioned above, all of the eggs were at approximately the same stage of development when obtained. In the latter large cluster, however, there was wide variation. Some eggs were in the early embryo stage with somites just beginning to form; others were in the eyed-embryo stages; and still others began hatching as soon as they were brought into the laboratory from outdoor oyster trays. This indicates that a large female clingfish presumably returns to the same shell on successive days and lays more eggs. Since no egg-bearing oyster shells ever contained more than one fish, it is improbable that two fish would share the same shell. As to relationship between age and position in the shell, the oldest eggs appear to occupy the middle portion.

When freshly laid and in early stages of

development, the eggs are bright yellow, due to the heavy yolk showing through the transparent, finely corrugated shell. Eggs in good condition were usually accompanied by a male *G. strumosus* that kept them constantly aerated by fanning anal and caudal fins. The male sex was ascertained by dissection in one case. Usually the eggs are ovate, though occasionally they are spherical or ovate-elongate. Under magnification they are seen to be somewhat flattened on the side where they are attached to the oyster shell, causing a discrepancy in the size of their lesser axis, depending in what position they are measured. This is taken into account in Table 1. Thus, the eggs averaged 0.67 × 0.94 mm to 0.75 × 0.94 mm depending on the axis of measurement. The early embryo does not seem to have any specific orientation in relationship to the egg's attachment, since it was observed in all positions; however, the fully developed embryo assumes a characteristic position of ventral side up. The distinctive features of the early, fertilized egg are compared with other species in Table 2.

(1) One group of eggs was taken from the floating box at 10:00 A.M. on June 26, 1960, about one-half to one hour after fertilization. The water temperature was 78° F. They were immediately transferred to a bowl of bay water which, taken to the Laboratory, was equipped with an aeration tube and pump. The eggs were kept under constant observation, and some were preserved every hour. At this time the eggs had already expanded from water hardening but had not yet begun cleavage (Fig. 2). The heavy yolk substance was simply a granular mass, having a multicellular appearance, with 70–80 small oil droplets present. The perivitelline space formed approximately 15–20 per cent of the egg. Probably the reason for the large size of the egg mass and the small size of the perivitelline space is that the egg has secure attachment on the bottom in quiet waters. Consequently, there is no need for protection against jarring or survival in rough waters as is necessary for pelagic type eggs such as those of the striped bass, *Roccus saxatilis* (Mansueti, 1958A:7).

(2) At two hours the eggs had begun their meroblastic cleavage and were mainly at the two-cell stage. The temperature was maintained at about 74–76° F after these stages had been attained.

(3) At three hours most of the eggs were at the four-cell stage. The blastodisc was already very prominent and the rounded blastomeres were well-defined units. The numerous oil droplets, which had been reduced to 30–60 but which had increased somewhat in size, were concentrated at the negative pole of the egg (Fig. 3).

(4) At four hours the eight-cell stage predominated. The blastomeres were still in a single layer, forming two rows of four cells each (Fig. 4).

(5) At five hours many of the eggs were in the 16-cell stage. Observed dorsally, the blastomeres comprised a well-contained, compact ring. This germinal area was comparatively large, forming about one-third of the actual egg substance (Fig. 5).

(6) At six hours the eggs were at the 32-cell stage and beyond. The amount of perivitelline space and the number of oil droplets were still quite constant (Fig. 6).

(7) At seven hours the cells were no longer countable though, judging by their relative size, they were probably between the 64–128-cell stage. Although the cells were smaller, the blastodisc still retained its previous volume.

(8) At eight hours the blastodisc had flattened somewhat and the developing egg had reached the morula stage, the cells forming a compact, berry-like mass (Fig. 7).

Due to hourly preservation and to the difficulty in teasing the eggs apart intact, this small supply of eggs became depleted at this point.

On May 24, 1961, at 10:30 A.M. another cluster of eggs was obtained at the end of gastrulation and at the beginning of neural groove formation, though some of the eggs were at the stages of the development of the embryonic shield and the downward expansion of the germ ring (Figs. 8–10). The water temperature was 66° F. Development proceeded in the Laboratory at 66–69° F, fluctuation due to temperature changes in the room. From comparison with other species at similar water temperatures, I would

TABLE 1.—Measurements of normal eggs of clingfish, *Gobiesox strumosus*, maintained at a temperature of 74–76° F, at the Chesapeake Biological Laboratory, Solomons, Maryland.

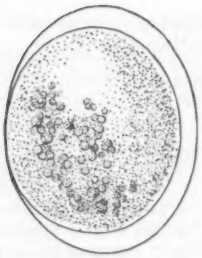
Age in hours	Number measured	Diameter in Millimeters of							
		Greater Axis		Lesser Axis[1]		Lesser Axis[2]		Yolk[3]	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
3–7	11	0.96	0.91–0.99	0.80	0.76–0.84	0.74	0.68–0.78	0.65	0.63–0.70
24	20	0.93	0.84–0.99	0.80	0.75–0.84	0.68	0.63–0.73	0.67	0.61–0.73
28	20	0.94	0.89–0.98	0.80	0.77–0.83	0.67	0.65–0.71	0.72	0.68–0.76
32	20	0.94	0.89–0.99	0.79	0.76–0.83	0.66	0.63–0.69	0.73	0.68–0.77
36	21	0.92	0.88–0.97	0.78	0.75–0.82	0.66	0.65–0.69	0.71	0.68–0.77
40	20	0.93	0.89–0.98	0.79	0.73–0.82	0.64	0.58–0.70	0.72	0.66–0.76
48	22	0.94	0.89–0.99	0.76	0.70–0.80	0.62	0.58–0.71	0.65	0.60–0.70
Total and Mean	134	0.94	0.88–0.98	0.79	0.75–0.83	0.67	0.63–0.72	0.69	0.65–0.74

[1] Measured with adhesive disc ventral to eggs.
[2] Measured with adhesive disc lateral to eggs.
[3] Measurements of yolk are based on eggs attached ventrally.

TABLE 2.—Comparison of the eggs of clingfish, *Gobiesox strumosus*, with those of ecologically similar species.[1, 2]

	Gobiesox strumosus	*Chasmodes bosquianus*	*Hypsoblennius hentz*	*Gobiosoma bosci*
Spawning period	April–August	April–August	May–September	June–October
Egg				
Shape	Ovate	Round	Round	Elliptical
Shell length	0.88–0.98 (0.94) mm	0.93–1.10 (1.04) mm	0.77 mm	1.15–1.37 mm
Shell width	0.75–0.83 (0.79) mm	0.80–0.90 mm, lateral	—	0.57–0.59 mm
Color	Bright yellow	Pale yellow	Pinkish	Yellowish, opaque
Oil globules	Numerous ca. 30–60, varying in size ca. 0.02–0.10 mm, concentrated at negative pole	Numerous ca. 15–40, ca. 0.01–0.10 mm, yellowish, mostly in half of yolk nearest positive pole	Usually 5–15, ca. 0.01–0.11 mm, golden yellow, concentrated near blastoderm	Numerous, minute
Yolk	Quite granular	Quite granular, dense opaque central body	Granular, violet and rose-colored bodies; large, dense, grayish central body	Greenish-yellow cast, Often lies toward pole opposite adhesive foot
Blastodisc	Very prominent, forms about one-third of egg mass	Prominent, about one-eighth of egg mass, next to adhesive disc	Prominent, about one-sixth of egg mass, next to adhesive disc	Prominent in early cleavage, about two-fifths of egg mass
Perivitelline space	15–20 per cent of egg volume, narrow or wanting at negative pole	Small at positive pole, very narrow or wanting at negative pole	Small at positive pole, very narrow or wanting at negative pole	Large, somewhat more than half of volume within egg membrane
Pigmentation of embryo	None on head or yolk, but body heavily marked	Slight on head, lightly on yolk and dorsum	Heavy on yolk	None on entire body

[1] Spawning period data for the other species is from Hildebrand and Schroeder (1928:323, 333, 335); all other information is taken from Hildebrand and Cable (1938:548–64, 576–89, 603–11).
[2] *Gobiosoma ginsburgi* and *Microgobius thalassinus* are not included in the table because the eggs are not described.



0.78 mm x 0.91 mm

Fig. 2

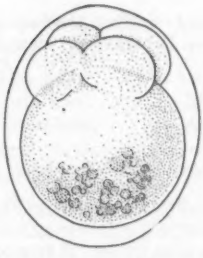


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Fig. 3

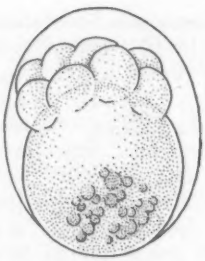

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Fig. 4

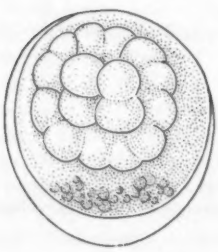

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Fig. 5

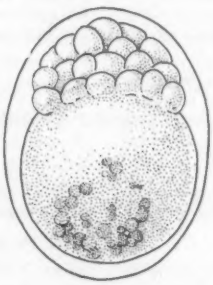

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Fig. 6

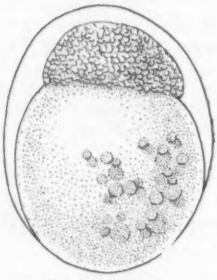

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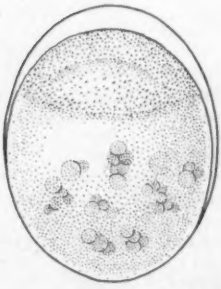
Fig. 7

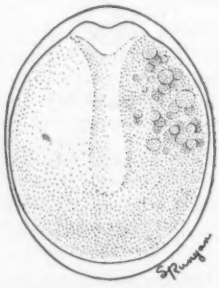


0.80 mm x 0.93 mm

Fig. 8

0.80 mm x 0.93 mm

Fig. 9



0.80 mm x 0.94 mm

Fig. 10

Figs. 2–10.—Early developmental stages of the eggs of the clingfish, *Gobiesox strumosus*.

Fig. 2.—Fertilized egg, before cleavage, 0.78 × 0.91 mm in diameter.

Fig. 3.—Fertilized egg, four-cell stage, 0.80 × 0.96 mm in diameter.

Fig. 4.—Fertilized egg, eight-cell stage, 0.80 × 0.96 mm in diameter.

Fig. 5.—Fertilized egg, 16-cell stage (dorsal view), 0.80 × 0.96 mm in diameter.

Fig. 6.—Fertilized egg, 32-cell stage, 0.80 × 0.96 mm in diameter.

Fig. 7.—Fertilized egg, many-celled stage or morula, 0.80 × 0.96 mm in diameter.

Fig. 8.—Fertilized egg, germ ring and embryonic shield stage, 0.80 × 0.93 mm in diameter.

Fig. 9.—Fertilized egg, early embryonic stage, 0.80 × 0.93 mm in diameter.

Fig. 10.—Fertilized egg, early embryonic stage (posterior view), 0.80 × 0.94 mm in diameter.

estimate that the eggs were approximately 20 hours old. This time they were kept in a bowl connected with a running salt water system. The male parent was present in the shell when it was taken and remained in it throughout the incubation period in the Laboratory.

(9) By approximately 24 hours the primitive streak and neural groove had extended almost halfway around the yolk substance; also, there were both a cephalic and a caudal swelling visible. Optic vesicles were forming. The numerous oil droplets remained clustered in the caudal region of the yolk (Fig. 11).

(10) By approximately 28 hours the yolk substance had become more spherical, and the embryo itself was well lifted off of its underlying yolk. Forebrain formation was quite evident. Then for several hours visible change took place very slowly (Fig. 12).

(11) By approximately 36 hours the embryo was wrapped two-thirds around the yolk substance. Midbrain development displayed itself as a prominent hump, and optic placodes were in the process of formation. The number of oil globules had been reduced to 10–20, with some showing considerable increase in size. Six to eight somites were becoming visible just behind the mid-body region (Fig. 13).

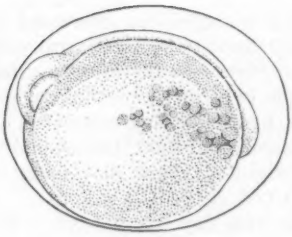
(12) By the third day the embryo had encircled three-fourths of the yolk circumference. Brain lobulation was clearly visible. The choroid fissure of the eye had developed. Auditory placodes were also present but small. A rudimentary heart was pulsating slowly but apparently vascular channels to the body had not yet been formed, as circulation was seen only in the heart region. About 15 somites were clearly defined in the caudal region but advancing forward became less distinct. The first pigmentation had appeared as a few, small melanophores above and below the notochord on the surface of the midbody region (Figs. 14A and B).

(13) In three and a half days the eyes had begun to undergo pigmentation. The auditory placodes were larger and more distinct. Vascularization had been achieved and circulation could be observed over the whole body. Oil globules had decreased in number to 4–10 droplets in the ventral yolk region. Somites were less distinct than before and visible only in the caudal region. Melanophores had increased somewhat in number, size, and definition. Occasionally, the embryo exhibited slight movement of the trunk and tail (Figs. 15A and B).

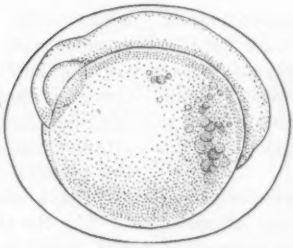
(14) By the fifth day the embryo virtually filled the egg, with the tail wrapping around the side of the body and the head region. The most prominent feature was the heavily pigmented eyes which, due to their blackness and immense size, dominated the interior of the egg. Two otoliths had formed in the auditory placode. The mouth was still undeveloped. The heart was situated in a frontal concavity of the yolk sac and was pulsating rapidly. The few, remaining oil globules were quite large. Somites were no longer visible. Pigmentation, in the form of rows of melanophores, was confined to the anterior two-thirds of the body behind the yolk. There was none on the head or the yolk (Figs. 16 and 17). The embryos were very active and at frequent intervals squirmed vigorously within the egg. Mansueti (1956A:137) noted that they "twitched" when stimulated by too much light.

(15) By the seventh day, just prior to hatching, the embryo was very cramped within the egg and had to wrap around itself in a coil. The mouth and external nares had developed. Most of the yolk had been absorbed. Pigmentation had become darker and more concentrated on the trunk. Some embryos had one or two very faint melanophores on the dorsum of the head behind the eyes.

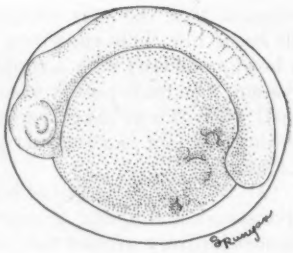
Just before hatching the embryo changed its position frequently. Because of lack of space within the egg, this movement required much manipulation. During one of these maneuvers there was suddenly a break in the chorion and the tail slipped out first. With a few short periods of rest and two or three more quick twists, the hatchling managed to free the rest of its body. Since the head emerged last, in some cases it became imprisoned momentarily inside the crumpling chorion (Figs. 18A, B, and C).



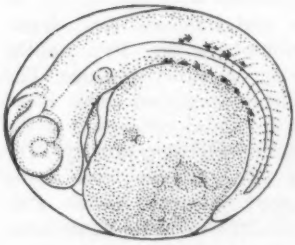
0.80 mm x 0.94 mm
Fig. 11



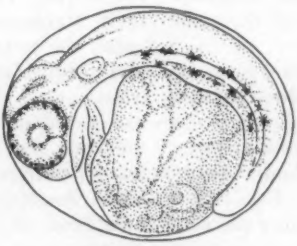
0.80 mm x 0.94 mm
Fig. 12



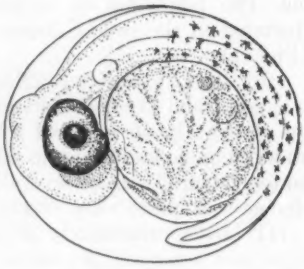
0.79 mm x 0.94 mm
Fig. 13



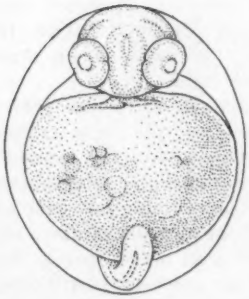
0.76 x 0.94 mm
Fig. 14A



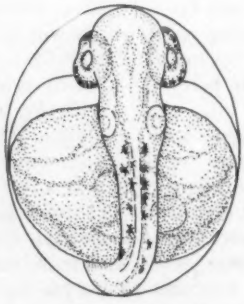
0.78 x 0.92 mm
Fig. 15 A



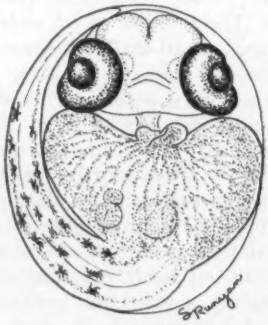
0.76 mm x 0.91 mm
Fig. 16



0.76 x 0.94 mm
Fig. 14 B



0.78 x 0.92 mm
Fig. 15 B



0.81 mm x 0.93 mm
Fig. 17

Figs. 11–17.—Developmental stages of the embryo in the eggs of the clingfish, *Gobiesox strumosus*.

Fig. 11.—Fertilized egg, early embryonic stage (lateral view), 0.80 × 0.94 mm in diameter.

Fig. 12.—Fertilized egg, early embryonic stage, 0.80 × 0.94 mm in diameter.

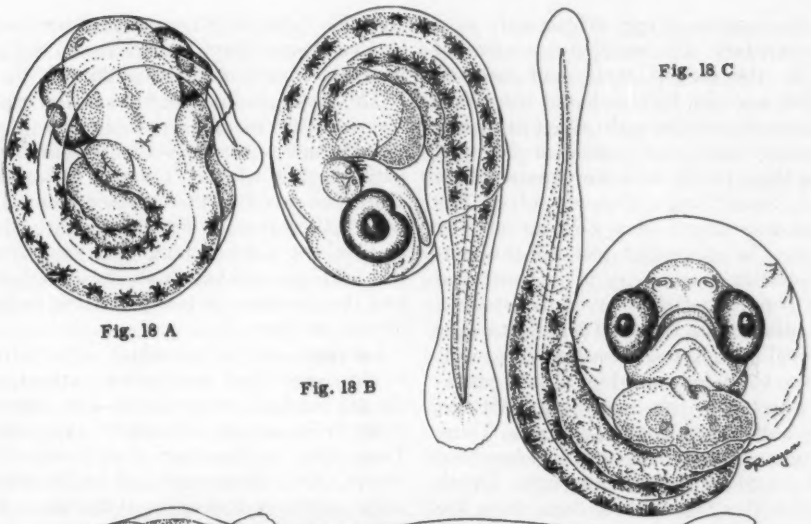
Fig. 13.—Fertilized egg, early embryonic stage, 0.79 × 0.94 mm in diameter.

Fig. 14.—Fertilized egg, developing embryo, 0.76 × 0.94 mm in diameter. A. Lateral view. B. Ventral view.

Fig. 15.—Fertilized egg, developing embryo, 0.78 × 0.92 mm in diameter. A. Lateral view. B. Dorsal view.

Fig. 16.—Fertilized egg, developing embryo, 0.76 × 0.91 mm in diameter.

Fig. 17.—Fertilized egg, well-developed embryo (ventral view), 0.81 × 0.93 mm in diameter.



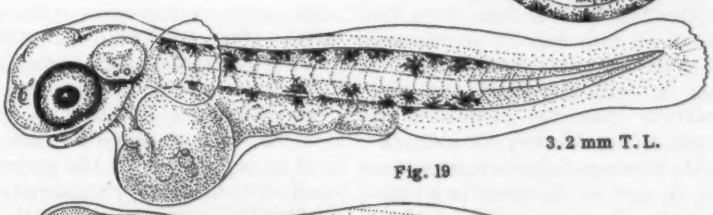
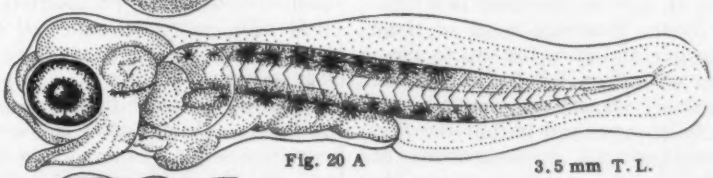


Fig. 19



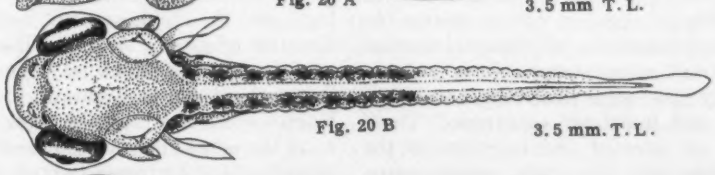
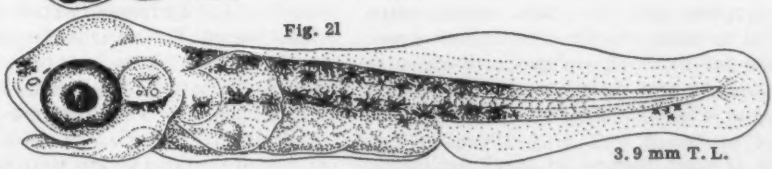


Fig. 21



Figs. 18–21.—Hatching of the embryo and larvae of the clingfish, *Gobiesox strumosus*.

Fig. 18.—Hatching of embryo, egg diameter 0.82 × 0.96 mm, larva 3.2 mm long. A. Dorsal view. B. Lateral view. C. Ventral view.

Fig. 19.—Prolarva, soon after hatching, 3.2 mm long.

Fig. 20.—Prolarva, 3.5 mm long, almost indistinguishable from early postlarva. A. lateral view. B. dorsal view.

Fig. 21.—Postlarva, 3.9 mm long.

Of two clusters of eggs which were kept in the same bowl at a water temperature of 66–69° F, the hinged shell contained an adult fish and the half-shell did not. With the former cluster the male clingfish moved continuously back and forth over the eggs, fanning them gently with his expanded fins (Fig. 1, foreground). The effects of this ceaseless movement were obvious after a few days. The eggs which received this constant aeration were kept in a clean and healthy condition and survived to hatching. On the other hand, the dead and dying eggs in the shell lacking the attention of an adult fish attracted *Glaucoma*-like ciliate protozoans which are free-swimming bacterial feeders, and the fungus *Saprolegnia*. These microorganisms were apparently associated with the asphyxiation of the eggs. Death occurred within two to three days, when the embryos were at the stage of developing pigmented eyes.

A number of well developed and pigmented embryos from the parent-tended shell were put in a petri dish for observation. The only aeration they were given was supplied by an airstone for about a minute every few hours. However, most of them managed to live and grow for two to three more days, when they hatched as normal larvae. This may suggest that once the embryos are fully developed within the egg, the adversely-altered microenvironment and debilitated eggs are not as susceptible to bacterial, protozoan, and fungal infection as they are at earlier stages.

In early dead eggs the embryo assumed a cloudy and indistinct appearance. There was also an internal disintegration of the oil droplets and the yolk, which often tended to ooze into the perivitelline space. In the pre-hatching embryo a decrease in the amount and intensity of melanophore material was an indication of death. Also, the eyes had a dull gray appearance in place of their former jet black brilliance. The yolk became a paler, duller yellow and was less clearly defined than in the live embryo.

Although I was not able to follow one complete series of embryos from fertilization to hatching, I would estimate the incubation period of *Gobiesox strumosus* to be five to seven days, depending on the temperature level in a range of 66°–76° F.

The distinguishing features of the eggs of *Gobiesox strumosus* are compared (Table 2) with those of ecologically similar species with which it is found. The eggs of *Gobiesox strumosus* can be differentiated from all of these other species by their ovate shape and, in the pre-hatching embryos, by the lack of pigmentation on the head and yolk, and the presence of many stellate melanophores on the body.

Larvae:—All larvae which were hatched in the large bowl simulating natural conditions hatched between 3.40–3.85 mm with their yolk already absorbed (Fig. 20A). Those kept in the petri dish hatched between 2.85–3.40 mm and still had relatively large yolk sacs measuring 0.26–0.57 mm in length (Fig. 19). Mansueti (1956A:142) illustrated a yolked stage somewhat similar to the latter group that averaged 3.5 mm. Perhaps the higher water temperature—75°F as opposed to 69°F—and the lower level of oxygen caused the embryos in the small dish to hatch prematurely. Pearson (1941:100), however, indicated they may be even smaller, although they are seriously questioned below.

In newly hatched prolarvae—the yolk-sac larvae (Hubbs, 1943:260)—the larval body was slightly curved, the head was high, and the trunk and tail had their axis directed relatively straight. The snout-to-anus length was somewhat beyond median, being about 60 per cent of the standard length, which is almost the same proportion as in the adult. The well-formed mouth extended almost horizontally back to the mid-orbital region. The nostrils were present but somewhat difficult to see because of the transparent nature of the head. The otocyst and otoliths were very distinct. The large, jet-black eyes, which composed about 52 per cent of the head length, were flecked with orange and green pigment. The transparent, outwardly projecting opercula could be seen only from a dorsal view. The pectoral fins, as well as the finfolds, were transparent and lacking in pigmentation; the tail was relatively short and spatulate. Melano-

phores were arranged in two definite rows, one above and one below the notochord on each side, stopping shortly beyond the anus. There was also one large melanophore along the ventral border of the otocyst. Myotomes in hatchlings numbered 21–23+ with 13 or 14 pre-anal. Because of heavy pigmentation, they were much more difficult to count in the trunk region than in the colorless tail region. This unpigmented region, important for diagnostic reasons, was apparently first observed by Pearson (1941:100). Constant peristalsis was evident in the comparatively large gut. Also, pulsation of the heart and circulation over the whole body was easily observable. There was no air bladder, a fact confirmed by Jordan and Evermann (1898: 2327), but this is a common condition among bottom-dwelling species (Fig. 19).

Although Mansueti's larvae, which did not hatch until about 3.5 mm (Mansueti, 1956A:142), still had yolk, those hatched by the author had already virtually absorbed their yolk by 3.5 mm (Fig. 20A). The pectoral fins, which were about 0.4 mm long, were well developed in shape and usage but were still completely transparent. During attempts to stain larvae of this size with alizarin Red S in order to check for possible osseous development, the pectoral fins appeared to have six to eight rays. Of 12 specimens only two absorbed any stain, which was diffused mainly through the notochord, the mandible, and branchial bars. Visible myotomes had increased from 14 to 15 preanal with a total of 27–29 but were much more distinct in the stained than in the unstained larvae. The large, stellate melanophores on the surface were now more distinct. There were about 10–15 of them situated along the dorsum of the body extending from the back of the head to about 0.35 mm beyond the anus (Fig. 20B). These were so large that their edges often fused with each other. There was also a definite row of them extending along the groove between the notochord and visceral mass and between the notochord and finfold. The gall bladder was obvious as a very conspicuous yellowish-green sphere, situated midway the length of the pectoral fin.

By 3.9 mm the postlarvae, which are the larvae between yolk-sac absorption and completion of fin-formation (Hubbs, 1943: 260), had become more slender in outline, the finfold having moved more caudad. The ventral surface of the body was noticeably straight in outline. Due to the opacity of the tissue, myotomes were no longer countable in the trunk region. Three or four small melanophores had appeared on the ventral finfold near the urostyle, and there was also some pigmentation between the nostrils. The trunk had acquired a chartreuse coloring. The jaws manipulated much better than in the younger larvae (Fig. 21).

Pearson (1941:100) stated in his observations that the young ranged from 2.0–4.5 mm in length and that they were rather broad, anteriorly depressed and posteriorly compressed, somewhat similar to the adult. This statement for the smaller individuals is in serious conflict with my observations and illustrations (Figs. 19–21), and I suggest that misidentifications at these sizes may have been involved.

The best diagnostic combination of characteristics of newly hatched *Gobiesox strumosus* that separates it from all other ecologically similar species (Table 3) are: (1) pigmentation in the form of large, stellate melanophore saddles numbering 10–15; (2) absence of pigment on the posterior third of the body; (3) a laterally compressed body with a broad head and a spatulate tail; and (4) a very large eye in proportion to the head length. Mr. William Dovel suggested to me that the transparent part of the finfold on the outer margins of the granulated finfold may be distinctive of the clingfish.

As compared with newly hatched *Gobiosoma bosci* and *ginsburgi*, *Gobiesox strumosus* is longer in total length, its eye is larger, its tail is spatulate instead of tapered, and it has much greater pigmentation. It can be distinguished from both *Chasmodes bosquianus* and *Hypsoblennius hentz* by a proportionately much longer snout-to-anus length and by more pre-anal and considerably fewer post-anal myotomes. It also lacks the long, slender tail and the pigmentation on the pectoral fin which is so obvious in both *Chasmodes bosquianus* and

TABLE 3. Comparison of early larval clingfish, *Gobiesox strumosus*, with ecologically similar species at hatching.[1]

	Gobiesox strumosus	*Chasmodes bosquianus*	*Hypsoblennius kentz*	*Gobiosoma bosci* and *ginsburgi*	*Microgobius thalassinus*
Hatching length in mm	ca. 2.8–3.5	ca. 3.6	ca. 2.6	ca. 2.0	ca. 1.7
Per cent snout-to-anus/ standard length	ca. 60.0	ca 40.0	ca. 42.0	ca. 64.0	ca. 52.0
Per cent head length/ standard length	ca. 21.0	ca. 27.0	ca. 24.0	ca. 24.0	ca. 24.0
Per cent eye length/ standard length	ca. 11.0	ca. 11.0	ca. 12.0	ca. 9.0	ca. 9.0
Per cent eye length/head length	ca. 52.0	ca. 41.0	cas. 48.0	ca. 43.0	ca. 37.0
Per cent total post anal/ standard length	ca. 48.0	ca. 69.0	ca. 68.0	ca. 40.0	ca. 55.0
Per cent yolk sac length/ standard length	ca. 16.0	ca. 16.0	Nearly all absorbed	ca. 24.0	—
Number of myotomes					
Pre-anal	13 or 14	8 or 9	3 or 4	12 or 13	12
Post-anal	12+	28–30	24–26	ca. 20	15
Total	25 or 26+	36–39	28–30	32 or 33	27
Number of adult vertebrae	27	33	33	ca. 27	ca. 27
Body shape	Head broad but trunk compressed laterally	Head and trunk short and robust, tail long and slender	Robust anteriorly with broad depressed head, tail long and slender	Rather slender and somewhat compressed	Robust anteriorly with deep head, slender and tapering posteriorly
Tail shape	Rounded spatulate	Rounded spatulate	Moderately tapered	Tapered	Flat-ended spatulate
Pigment on posterior 30 per cent of body	None	One spot per myotome along base of ventral finfold	One spot per myotome along base of ventral finfold	Few small spots at base of ventral finfold	One or two spots on ventral outline
Melanophore design	Two large rows preanal and a little post-anal, one under otocyst	Many along upper margin of abdomen and on pectorals, along base of ventral finfold	Many over abdominal region and on pectorals, under otocyst, along base of ventral finfold	Few spots over vent and at base of ventral finfold posterior to vent	Several spots on ventral outline

[1] Information is taken from Hildebrand and Cable (1938:548–64, 576–89, 603–11).

Hypsoblennius hentz. It is easily separable from *Microgobius thalassinus* by having a much greater total length, a much larger eye in relationship to the head length, and much heavier pigmentation.

The larvae moved by quick darts interspersed with periods of rest when they fell over on their sides motionless; in fact, they seemed unable to maintain upright balance unless they were moving. At first they hovered near the surface of the water, but by the second day much of their movement was confined to the bottom. Most of the time, up and down movements were accomplished with the body in a vertical position. In gaining the bottom the larvae went head first, letting the weight of their bodies carry them down. This coasting undoubtedly conserved energy. Numerous microscopic crustaceans were introduced into the water by fresh bottom mud. The larvae were observed nipping at the moving particles and were presumably feeding.

It was impossible to raise the larvae beyond 3.9 mm, and the cause of death could not be determined. It was presumed that they starved to death as suggested by Mansueti (1956B:4). Therefore, the important transformation from larvae to young, i.e., 3.9 to 12 mm, was not observed. Neither is this process recorded anywhere in the literature, although Pearson (1941:100) implied that his samples included some fish in this size range. His remarks, which must be appraised in context with the criticism given above, are as follows:

> "The young ranged from 2 to 4.5 mm in length. They are rather broad, anteriorly depressed and posteriorly compressed, somewhat similar to the adult. The body pigmentation is heavy, consisting of diffuse chromatophores very similar in arrangement to those on the young tautog (*Tautoga onitis*). The posterior caudal region of both species remains free from pigment.
>
> "Larval *Gobiesox* resembles larval *Tautoga* closely. Care is essential in distinguishing the larval fish of these two species, which are at times found to occur simultaneously in the plankton. Young *Gobiesox* possesses a less distinctive chromatophore pattern and the pigmentation does not extend so far back on the body as in *Tautoga*. *Gobiesox* also has a shorter gut and lacks the black-tipped upper jaw most characteristic of young *Tautoga*."

Springer and Woodburn (1960:85) collected specimens 8.5 mm in April and June, and suggested a spring and summer spawning period in Florida. They also collected a 10 mm specimen in a tide pool where the salinity was 27.2 ‰ and the temperature was 37°C.

Young:—The smallest transformed clingfish observed was 12 mm long. It showed a characteristic tadpole shape in dorsal outline (Fig. 22A). However, the head had not yet become broad and depressed. Dorsally it was shaped somewhat like a rounded triangle with the greatest width being at the opercles. The body itself tapered gradually to the compressed caudal peduncle.

The snout was becoming more shallow but the forehead still had a rather steep slope. The upper lip was scalloped, as was the premaxillary fold above it. The prominent premaxillary groove was an interesting feature, giving the illusion of a secondary mouth. Eight sensory barbels had appeared on the ventral surface of the lower lip. The mouth itself was now wide, inferior, and horizontal; and its gape extended as far back as the anterior margin of the eye. The eye was still lateral but had become much smaller in proportion to the head. Medial to the eye at its anterior margin was the tubular posterior nostril, a characteristic of this family (Briggs, 1955:8). The anterior nostril was the larger and was supplied with a peculiar bilobed, dermal flap attached to its posterior edge. Behind the eye were three definite pores arranged in a triangular pattern (Fig. 22B). Briggs (1955:8) intimated that these are part of the lateral line system. There were also about 10 more pores scattered over the head in various places, two of them being on the ventral surface halfway between the chin and the branchiostegal rays (Fig. 22C).

The upper margin of the gill membrane became continuous with the base of the pectoral fin opposite the sixth or seventh pectoral ray. Although the gill opening was somewhat restricted and mostly lateral, the gill membrane was free across the isthmus but overlapped slightly by the anterior margin of the adhesive disc.

The fins were already fairly well developed but were still quite transparent with no pigmentation present except for a few scattered melanophores on the pelvic fins.

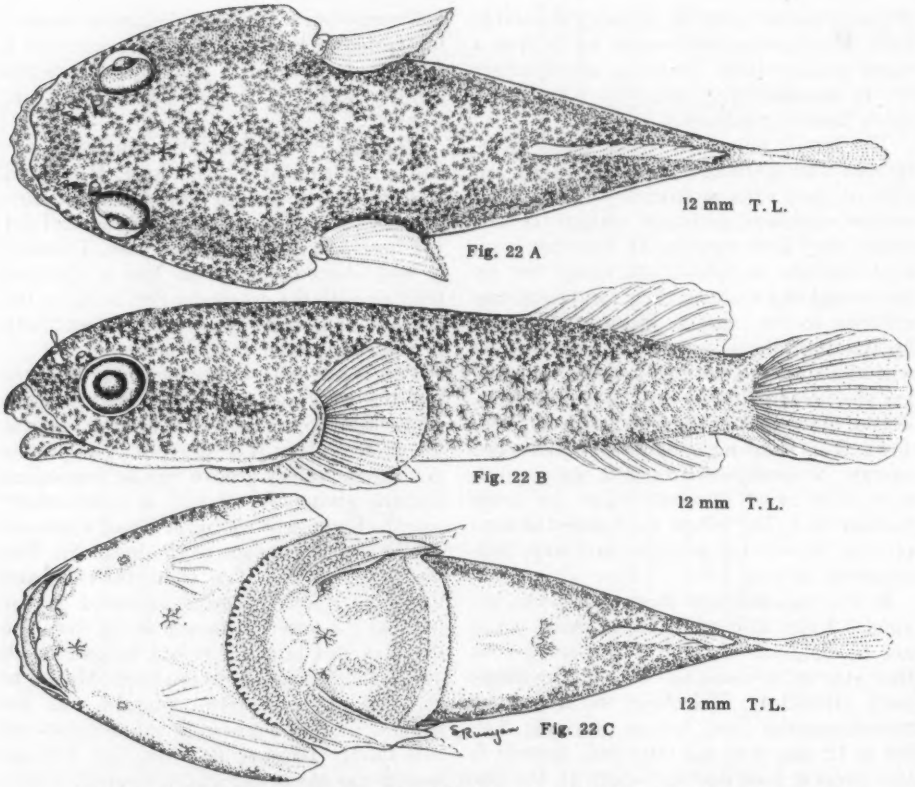


Fig. 22.—Advanced transformed young of the clingfish, *Gobiesox strumosus*, 12 mm long: A. dorsal view; B. lateral view; and C. ventral view.

Although the full complements of six branchiostegal rays and four pelvic fin rays had been reached, the other fins were still lacking one or two of their average observable number of rays. Sandwiched between the pectoral fin and the body was a smaller accessory flap which was an upward projection of the posterior portion of the adhesive disc. This was the axial dermal flap mentioned by Briggs (1955:8). The pelvic fins had been modified to help form this unusual disc.

The anterior margin of the modified pelvic or adhesive disc was bordered with a single row of approximately 30 coarse cirri, with some slight crennulations before blending with the edge of the pelvic fin. Both anterior and posterior collars of the disc were covered with six to eight staggered rows of indistinct papillae which increased in size the closer they were to the center of the disc. Parts of the pelvic fins and two fleshy pelvic pads were also covered with these minute papillae (Fig. 22C) which probably aided the gripping action, though one worker suggested that they might contain mucus glands. The central section of the disc was transparent enough for the outlines of the pectoral girdle and also the liver and other digestive organs to be observed through it.

As for pigmentation, the 12 mm long specimen of *Gobiesox strumosus* was in the process of changing from spotted larval to the reticulated adult patterns. Its dorsal and lateral surfaces were stippled with numerous stellate melanophores (Figs. 22A and B), but these had not yet formed the

definite reticulated arrangement, as they do in the adult. The undersurface was pale with only a few branching melanophores scattered randomly. Usually there were some around the anus, which was otherwise still quite indistinct; for the urogenital papilla was very small.

At 20 mm the young *Gobiesox strumosus* was quite stocky in shape. The percentage of greatest depth, which was measured at the opercular region, as against standard length was generally the greatest between 16 and 24 mm (Table 6). By now the head had become broader and the snout more blunt. The lower lip had 12 distinct papillae on its undersurface. As the head broadened and flattened, the eye was becoming less lateral. The caudally-directed subopercular spine which was hidden in the skin was, nevertheless, already quite prominent. Although the median fins were more fleshy, they were still somewhat flat and without flare. The papillae on the adhesive disc were much more distinct, and the disc itself had a more sturdy and definitive shape. Over the whole body the melanophores were becoming smaller and less distinct and were beginning to fuse into faint patterns. Three or four darker streaks radiated from the orbital region, and a few scattered bars of pigment were present on the dorsal, anal, and caudal fins. Rugal folds were developing around the anus.

Adult:—Although *Gobiesox strumosus* can attain a length of 65–70 mm, by the time it is 40–45 mm in total length it can be considered an adult; for this seems to be the average size of gravid fish during spawning season. The adult is characterized by a broad, depressed head which forms one-third of the total body length and by its large, unique adhesive disc. Scales are absent.

The forehead has become shallow and the snout very blunt. The upper lip juts beyond the fleshy lower one, where the 12 papillae stand out erect. By now the eye is small and somewhat superior. The interorbital is broad and flat, its width being approximately one-third of the greatest width of the head (Table 4). The head pores are still present but no longer as obvious as in the young. In the adult the cheeks are bulging, the opercle ending in the sharp preopercular spine which, according to Gregory (1933:427) serves as an accessory brace for the pelvic adhesive organ. The disc and pelvic fins have a wide flare. The unpaired fins are fleshy and widespread, while the pectoral fins remain rather membranous and delicate (Figs. 23A, B, and C).

There is a wide variation of pigmentation and coloration among individuals. Some examples of this can be seen in Fig. 1. This species seems to be able to change its coloration, ranging from pale ochre to dark olive brown. The surface to which they are attached, the water temperature, response to other external stimuli, and the secretion of slime all appear to affect coloration. However, there are undoubtedly specimens which remain generally lighter or darker than others (Hildebrand and Schroeder, 1928:339). Concentrations of melanophores in reticulations along the lateral surface of the body make up the most distinctive pigment pattern of the clingfish (Fig. 23B). A contrast to the dorsal surface of the body is the pearly tints of the ventral surface, on which melanophores are comparatively sparse. The disc papillae grow more distinct with age and change from white to bright yellow in color.

In the adult the base of the tail is quite dark, while the caudal fin itself often has three or four uneven bands of melanophore concentration. The dorsal and anal fins, especially, vary greatly in pigmentation. In some specimens they are almost white with darkening only at the base of the rays. Others are covered with dusky blotches forming barred patterns. The pectoral and pelvic fins remain generally pale, though sometimes there are small melanophores distributed along the edges of the fin rays (Fig. 23B).

Under the microscope one can observe areas of bluish-green, rust, and gold in the olive-brown background; the operculum is rosy, due to the gills beneath. However, the delicate shades of coloring in the clingfish are lost when it is preserved. Except for the pale undersurface, formalin turns the specimen a homogenous grayish-brown, which is relieved only by the dark pigment patterns; alcohol seems to give a yellowish cast.

TABLE 4.—Measurements of larval and young clingfish, *Gobiesox strumosus*.

Size intervals (T.L.) mm	Number of fish	Average Measurements in Millimeters													
		Total Length	Standard Length	Head Length	Head Width	Greatest Depth	Snout-to-Anus	Eye Length	Interorbital Width	Disc Length	Disc Width	Chin to Disc	Disc to Anus	Anus to Anal Fin	Yolk Sac Length
2.5-3.0	3	2.90	2.69	0.56	—	0.56	1.60	0.29	—	—	—	—	—	—	0.43
3.0-3.5	19	3.23	3.01	0.71	—	0.62	1.71	0.34	—	—	—	—	—	—	0.37
3.5-4.0	11	3.56	3.33	0.76	—	0.65	1.91	0.37	—	—	—	—	—	—	0.34
4.0-4.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4.5-5.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.0-5.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.5-6.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.0-6.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.5-7.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7.0-7.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7.5-8.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.0-8.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.5-9.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.0-9.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.5-10.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10.0-11.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11.0-12.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12.0-13.0	4	12.60	10.04	4.12	3.67	2.26	6.78	0.82	1.12	2.92	2.57	2.76	2.18	0.61	—
13.0-14.0	3	13.73	10.81	4.29	4.03	2.35	7.10	0.88	1.20	3.26	2.82	3.02	2.08	0.79	—
14.0-15.0	1	14.30	11.42	4.49	4.03	2.45	7.44	0.91	1.20	3.46	2.59	3.22	2.02	0.86	—
15.0-16.0	3	15.75	12.37	5.53	4.74	2.90	8.35	1.09	1.30	4.18	3.73	3.49	2.43	0.70	—
16.0-17.0	2	16.42	12.80	5.27	4.94	3.14	8.50	1.12	1.46	4.08	3.40	3.54	2.47	1.01	—
17.0-18.0	3	17.53	13.72	5.68	5.58	3.12	9.23	1.14	1.50	4.61	3.90	3.83	2.58	1.04	—
18.0-19.0	3	18.88	14.79	5.74	5.81	3.14	9.89	1.23	1.65	4.98	4.04	3.80	3.25	0.90	—
19.0-20.0	2	19.48	15.19	6.37	6.36	3.38	10.01	1.21	2.06	5.22	4.58	3.44	2.40	1.12	—
20.0-22.0	2	20.80	16.34	6.83	5.92	3.76	10.48	1.22	1.81	5.12	4.46	2.10	1.60	1.15	—
22.0-24.0	2	23.09	18.02	7.10	7.44	4.18	12.10	1.32	1.92	5.93	5.38	4.58	3.68	1.08	—
24.0-26.0	3	24.75	19.41	7.09	8.07	3.92	12.81	1.46	2.57	6.82	5.98	5.16	3.75	1.30	—
26.0-28.0	2	26.16	20.74	7.68	8.26	4.37	13.03	1.44	2.30	6.46	5.98	5.40	3.76	1.26	—
28.0-30.0	2	29.28	23.33	8.46	9.28	4.88	14.98	1.62	3.16	8.06	7.32	5.86	4.60	1.50	—
30.0-32.0	2	31.43	24.48	10.56	10.54	5.10	16.52	1.95	2.51	8.93	7.99	6.45	4.95	1.72	—
32.0-34.0	5	33.17	26.24	10.04	10.52	4.85	17.27	2.00	2.90	9.36	7.47	6.84	5.63	1.85	—
34.0-36.0	2	34.88	27.19	11.22	10.88	4.65	18.52	2.02	3.56	9.98	8.36	6.75	6.34	1.50	—
36.0-38.0	4	36.72	29.43	11.90	11.47	5.30	19.16	1.99	3.78	10.26	8.68	6.68	5.55	2.14	—
38.0-40.0	2	39.00	30.64	12.45	12.34	5.52	20.44	1.99	3.72	10.72	8.25	7.24	6.98	2.40	—
40.0-42.0	4	40.80	33.31	12.81	12.54	5.98	21.64	2.11	3.72	10.97	9.35	8.66	6.83	2.16	—
42.0-44.0	2	42.92	34.39	14.10	13.46	6.42	23.50	2.25	3.83	11.29	10.02	9.00	7.65	2.29	—
44.0-46.0	3	45.55	36.25	15.30	14.35	6.23	24.66	2.48	4.40	12.47	10.27	9.98	7.84	2.35	—
46.0-48.0	3	46.95	37.65	15.85	15.15	6.05	25.33	2.38	5.20	12.75	11.13	9.80	7.97	2.29	—
48.0-50.0	3	48.75	38.73	15.38	16.30	7.68	26.20	2.35	4.63	13.53	12.45	10.75	7.90	2.42	—

The general behavior of clingfish was observed with live specimens in an indoor aquarium. Most of their time is spent adhering to the undersurface of empty oyster shells. From these hiding places they snap at any unsuspecting prey, such as amphipods, which swims too close. They may remain on the same shell for hours at a time, where their only movement is a gentle fanning of the tail. Occasionally, quick, agitated sallies are made into the sand, where their speckled coloring creates an effective camouflage. Once they have found a favorable location, they seem to cover very little distance. Only occasionally do they swim around above the shell layer but usually dart from one shell to another (or cling to the sides of the tank). Gravid fish, however, appear to be much more restless and move about rapidly and continuously.

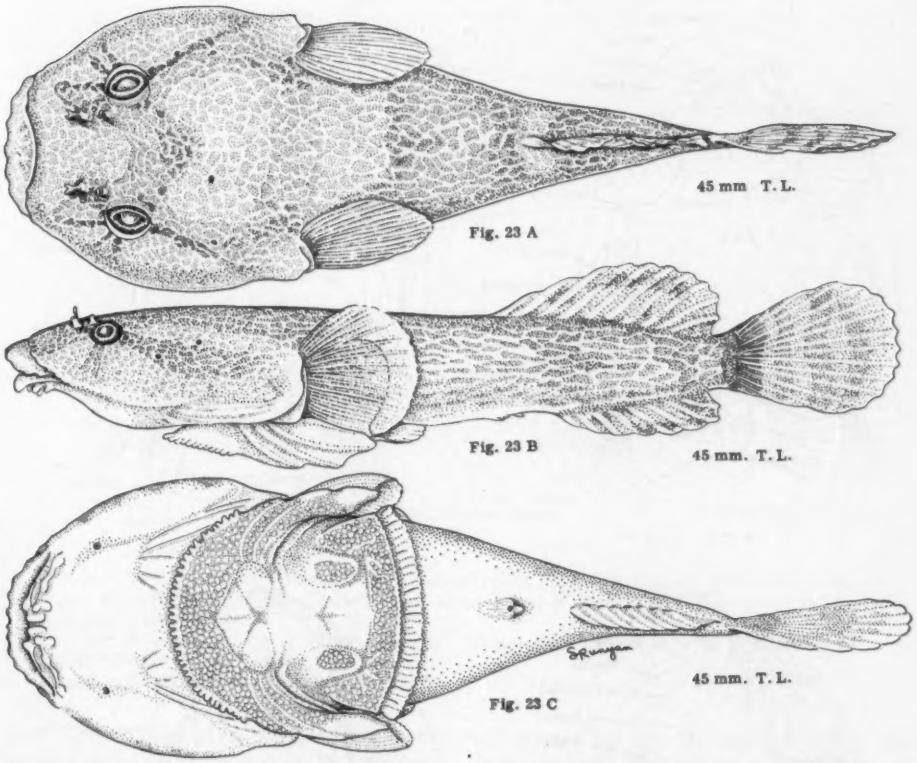


Fig. 23.—Adult of the clingfish, *Gobiesox strumosus*, 45 mm long: A. dorsal view; B. lateral view; and C. ventral view.

The clingfish is a very tenacious creature; for when one tries to catch an individual, it immediately clings stubbornly to whatever surface is near and can only be pried loose with difficulty (Longley and Hildebrand (1941:283). Even after the fish dies, the disc mechanism still retains a vestige of its adhesive powers. At the same time the clingfish exudes a thick, protective mucus which makes it very slippery and which also reacts with formalin to form a thick, white coating over the skin. This coagulated slime presents a problem in preservation, for it has to be scraped off patiently before details of the fish can be observed.

According to Hildebrand and Schroeder (1928:340), as shown by their investigation of the contents of 26 stomachs, the food of *Gobiesox strumosus* consists mainly of isopods and amphipods and also an occasional annelid. The stomachs of 20 specimens dissected during the present study revealed only amphipods. Live clingfish observed in the aquarium fed voraciously upon live amphipods and young sticklebacks up to 15 mm long, the only food offered to them. One specimen, however, attempted unsuccessfully to engulf a grass shrimp, *Palaemonetes*, approximately 20 mm long.

Osteology:—Seven specimens varying in size from 12 mm to 63 mm were cleared and stained by combining and modifying methods as prescribed by Fish (1932:296–7), Hollister (1934:89–100), Davis and Gore (1947:12–5), and Mansueti (1958B:2). The two above size extremes are illustrated in Figs. 24–27.

The fresh specimens were first put in a solution of 2 per cent KOH for several hours, then transferred to the staining solution, which consisted of 5 cc of alizarin Red

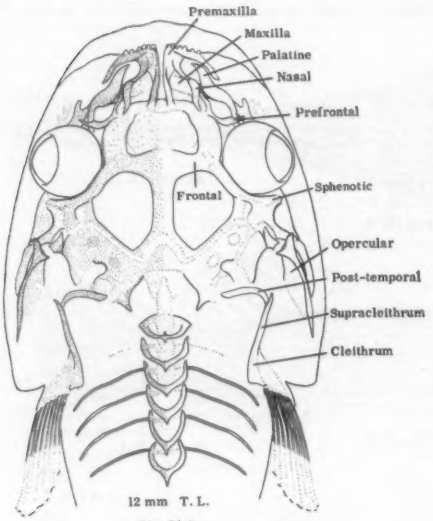


Fig. 24 A

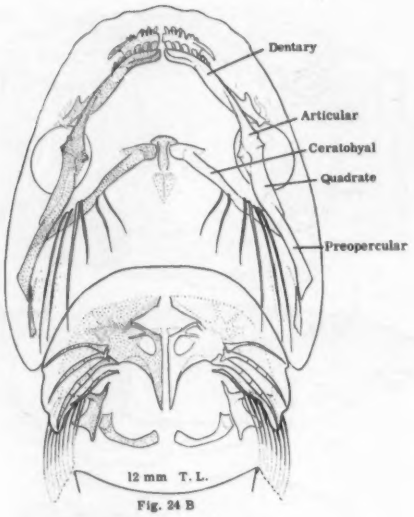


Fig. 24 B

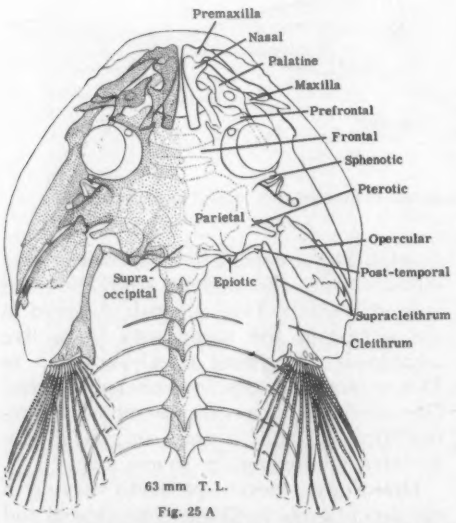


Fig. 25 A

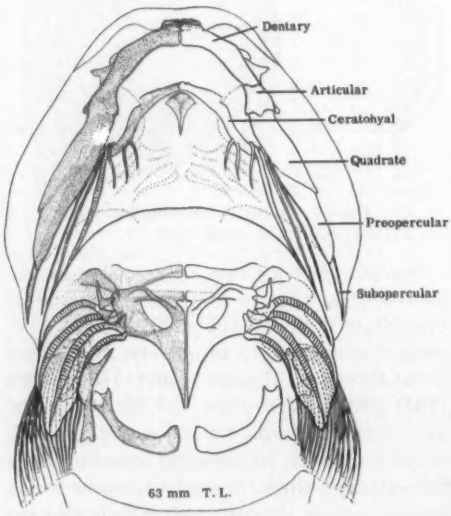


Fig. 25 B

Figs. 24–25.—Ossification in young and adult clingfish, *Gobiesox strumosus*, showing details of the skeletal structure in the head and pelvic girdle. Stippling shows the density of alizarin Red S stain. Views: A. dorsal; and B. ventral. The source for identification of osseous structures was Gregory (1933:373–4).

Fig. 24.—Drawing of young clingfish, 12 mm T.L.

Fig. 25.—Drawing of an adult clingfish, 63 mm T.L.

S per 1,000 cc of 2 per cent KOH. This proportion was varied according to the apparent strength of the staining reaction. After two or three days, when all osseous structures were well stained, the specimens were placed in 2 per cent KOH until the color was bleached out of the soft tissues; then they were gradually transferred to five gradu-

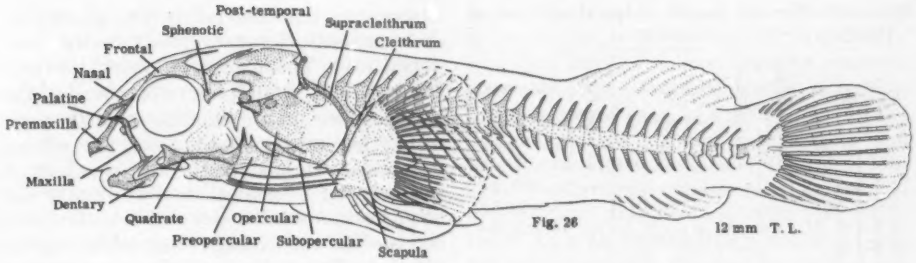


Fig. 26

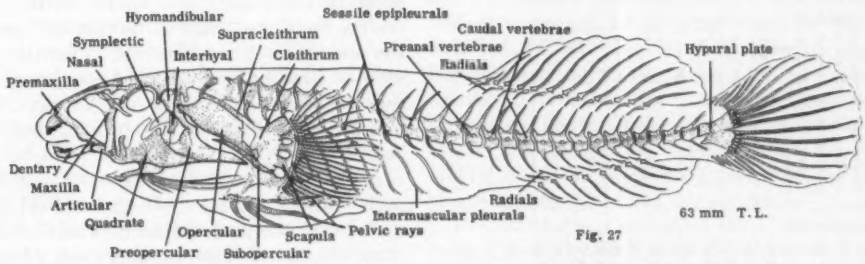


Fig. 27

Figs. 26–27.—Skeletal structure in the body of young and adult clingfish, *Gobiesox strumosus*, where stippling shows the density of alizarin Red S stain. The nomenclature follows Gregory (1933:373–4).

Fig. 26.—Lateral view of a young clingfish, 12 mm long. Dotted lines show unossified fin rays.

Fig. 27.—Lateral view of an adult clingfish, 63 mm long.

ated concentrations of increasing glycerin content and finally stored in 100 per cent white glycerin. Because of the unusual dorsally compressed thickness of the clingfish, the last clearing stages took several days longer than the time suggested by the above mentioned authors. Modifications in the strength of the various chemicals were necessary due to the relatively small size of the specimens.

Branchiostegal Rays:—As early as the 12 mm fish, the full complement of six branchiostegal rays is present and very well developed (Table 5 and Fig. 24B). These rays have their attachment on the ceratohyal bone (Gregory, 1933:374). The two most median rays are attached on the caudal side of the skeletal bar and the other four attached on the cephalic side. Although the three most median rays are short and the other three long, the rays seem to be attached in groups of two, the fourth ray from the midline always being the largest. This characteristic pattern was consistent in all of the 62 young and adult specimens studied, except for one 29 mm fish which had only five rays; and in this specimen the normal ray position was shifted. The branchiostegal rays are usually very easy to see except in the larger fish, in which the most lateral ray is often overshadowed by the thickened preopercular bone and submerged by the increasing fleshiness of the ventral surface of the head.

Pectoral Fin:—In the specimens on which counts were made, the number of pectoral rays ranged from 20–25 (Table 5), the breakdown being as follows: 20 rays were found in four fish, 21 in eight, 22 in twenty-four, 23 in twenty-one, 24 in eight, and 25 in one specimen. All fish having only 20 or 21 pectoral fin rays were less than 21 mm in length, except for one fish of 29 mm which possessed only 20 rays. Beyond 21 mm there seems to be no correlation between the number of pectoral fin rays and the further growth of the fish, as fins numbering 22–24 rays were fairly evenly distributed among all sizes, although 24 rays first appeared in

TABLE 5.—Meristic counts of larval and young clingfish, *Gobiesox strumosus*.

Size intervals (T.L.) mm	Number of fish	Branchiostegal Rays	Pectoral Fin	Pelvic Fin	Dorsal Fin	Anal Fin	Caudal Fin	Myotomes	
								s/a	total
2.5–3.0	3	—	—	—	—	—	—	13.3	21.7+
3.0–3.5	19	—	—	—	—	—	—	13.9	24.5+
3.5–4.0	11	—	—	—	—	—	—	14.7	28.0+
4.0–4.5	—	—	—	—	—	—	—	—	—
4.5–5.0	—	—	—	—	—	—	—	—	—
5.0–5.5	—	—	—	—	—	—	—	—	—
5.5–6.0	—	—	—	—	—	—	—	—	—
6.0–6.5	—	—	—	—	—	—	—	—	—
6.5–7.0	—	—	—	—	—	—	—	—	—
7.0–7.5	—	—	—	—	—	—	—	—	—
7.5–8.0	—	—	—	—	—	—	—	—	—
8.0–8.5	—	—	—	—	—	—	—	—	—
8.5–9.0	—	—	—	—	—	—	—	—	—
9.0–9.5	—	—	—	—	—	—	—	—	—
9.5–10.0	—	—	—	—	—	—	—	—	—
10.0–11.0	—	—	—	—	—	—	—	—	—
11.0–12.0	—	—	—	—	—	—	—	—	—
12.0–13.0	4	6.0	21.5	4.0	9.8	8.0	12.5	—	—
13.0–14.0	3	6.0	21.3	4.0	9.3	7.7	13.0	—	—
14.0–15.0	1	6.0	23.0	4.0	10.0	8.0	12.0	—	—
15.0–16.0	3	6.0	21.7	4.0	10.0	7.7	14.0	—	—
16.0–17.0	2	6.0	21.5	4.0	10.0	7.5	14.0	—	—
17.0–18.0	3	6.0	21.7	4.0	10.3	8.0	14.7	—	—
18.0–19.0	3	6.0	22.7	4.0	10.0	7.7	14.3	—	—
19.0–20.0	2	6.0	21.0	4.0	10.5	7.5	13.0	—	—
20.0–22.0	2	6.0	21.0	4.0	10.0	7.0	12.0	—	—
22.0–24.0	2	6.0	22.5	4.0	11.0	8.0	13.5	—	—
24.0–26.0	3	6.0	23.7	4.0	10.7	8.0	14.7	—	—
26.0–28.0	2	6.0	22.5	4.0	10.5	8.0	15.0	—	—
28.0–30.0	2	5.5	21.0	4.0	9.5	7.0	15.0	—	—
30.0–32.0	2	6.0	22.5	4.0	10.0	8.5	14.0	—	—
32.0–34.0	5	6.0	22.8	4.0	10.2	8.2	14.2	—	—
34.0–36.0	2	6.0	23.5	4.0	10.5	8.5	15.0	—	—
36.0–38.0	4	6.0	22.5	4.0	9.8	7.8	15.0	—	—
38.0–40.0	2	6.0	23.5	4.0	10.0	8.0	13.5	—	—
40.0–42.0	4	6.0	22.5	4.0	9.8	7.5	15.2	—	—
42.0–44.0	2	6.0	23.0	4.0	10.5	8.5	15.0	—	—
44.0–46.0	3	6.0	23.0	4.0	10.7	8.0	14.7	—	—
46.0–48.0	3	6.0	23.7	4.0	10.3	8.3	14.7	—	—
48.0–50.0	3	6.0	22.3	4.0	10.0	8.0	14.0	—	—

a specimen of 33 mm. However, the one fish possessing 25 rays was only 24 mm long.

Judging from the above data, one could assume that the clingfish has acquired its full complement of pectoral rays by the time it is about 20 mm long. However, the above information was obtained from observations made on regular, unstained specimens. The pectoral fin rays are sometimes difficult to count because the most ventral rays are obscured by the edges of the adhesive disc and the pelvic fin, as well as growing much closer together than the more dorsal rays. Though more slender, the ventral rays may actually develop ahead of the others, since in the smaller stained specimens they were denser than the others. Specimens stained with alizarin Red S showed that a greater number of rays are acquired at a smaller size and that the number is often the average observable number plus two. This is due to the fact that stained specimens revealed two small, extra rays, one on the dorsal edge of the fin and one on the ventral edge, which are generally not seen or counted in unstained specimens. Of the treated samples one had 23 rays, five had 25 (including the 12 mm fish), and one had 26.

All of the above data agrees fairly well with other authors. Briggs (1955:116) stated that the pectoral fin rays of *Gobiesox strumosus* number 24, ranging from 22 to 26. Schultz (1944:68) gave 23 as the number, while Longley and Hildebrand (1941:284) indicated that their counts, based on five specimens 30–70 mm long, ranged from 21–23. Jordan and Evermann (1898:2333) gave the lowest count, stating it as 21. It is possible that Briggs (1955:5) included the two tiny rays in his counts, whereas the other authors did not; for in my own observations approximately four-fifths of my unstained specimens fell within the 21–23 range.

Pelvic Fin:—The number of pelvic fin rays remains constant at four (Table 5).

The axial dermal flap between the pectoral fin and the body is actually part of the disc complex. This delicate, inconspicuous structure contains approximately 30 rays, but these must be only slightly cartilaginous; for they did not stain.

Dorsal Fin:—The dorsal and anal fin rays seem to be late in acquiring the full complement (Table 5). In the 12 mm stained specimen the dorsal rays were not yet ossified enough to absorb any stain, and the anal rays were only faintly stained; whereas at this point all of the other fins had very well developed rays (Fig. 26). The meristic count for the dorsal fin had a range of 9–11 with the breakdown being as follows: eight had 9 rays, forty-three had 10, and fifteen had 11. Although ossification

is late, the dorsal fin appears to possess a full number of rays by the time the fish reaches 12 mm in length; for the first specimen with 11 rays was only 16 mm long, and the last with only 9 rays was 41 mm. Staining showed that at the cephalic end of the dorsal fin there is a tiny, almost subcutaneous fin ray present. This small ray was not included in the regular counts. However, it was probably included by Hildebrand and Schroeder, Briggs (see statement under *Anal Fin*), and Schultz, as these authors averaged one or two more rays than I did. Jordan and Evermann (1898:2333) stated their count as 11, and Longley and Hildebrand (1941:284) as 10 or 11, which agrees with mine.

Anal Fin:—The range for anal fin rays (Table 5) was 7–9, thirteen fish having 7 rays, forty-seven having 8, and six having 9. The stained fish confirmed this count, but revealed a very small ray at the cephalic end of the fin. Just as in the dorsal fin, this rudimentary ray was not included in the regular count. Hildebrand and Schroeder (1928:339) gave their range as 8–10, nine-tenths of their specimens having 8 or 9 rays; Longley and Hildebrand (1941:284) agreed on 8 or 9 rays, and Schultz (1944:68) on 9. However, Briggs (1955:116) stated his count as falling between 9 and 11 and Jordan and Evermann (1898:2333) as 10. They were no doubt including the rudimentary ray, especially since Briggs (1955:88), in speaking of the genus *Gobiesox* made the following statement:

> "Usually the first 2 dorsal and anal rays are very much reduced, and are not externally visible except on comparatively small specimens in which the fin membranes are thin and semi-transparent. Sometimes only the first ray in each fin is so reduced, as is the case in some examples of *G. strumosus*. . . . For identification, when time for dissection or clearing and staining cannot be spared, it is usually safe to add 2 to the external dorsal and anal ray counts in this genus."

In this fin also there seems to be no correlation between growth and the number of fin rays beyond the 12 mm stage; for the first specimen with 9 rays was only 13 mm long and the last one with 7 rays was 41 mm in length.

Caudal Fin:—Meristic counts on the caudal fin (Table 5) of the clingfish are generally not useful because of the difficulty in setting up a reliable criterion by which to count the caudal rays. Therefore, most authors disregard them in their counts. Of the aforementioned authors, only Jordan and Evermann (1898:2333) and Briggs (1955: 116) bothered to mention the number of caudal rays; this count Jordan and Evermann gave as 16 and Briggs as 12 (11–13) for principal rays. The problem is that unless one stains each specimen or strips the flesh from its tail, an accurate count is difficult. Mr. William Dovel, of the Chesapeake Biological Laboratory, in working with the toadfish, *Opsanus tau*, encountered a similar difficulty. To facilitate ray and vertebral counts, he boiled his specimens in dilute NaOH until the macerated flesh was easily removed from the bony structures.

I found that the principal rays—those attached to the hypural plate—number 10–12; and secondary rays also have a range of 10–12, 5 or 6 being situated dorsal and ventral to the principal rays and more cephalad. In my stained specimens the number of principal and secondary rays in different combinations produced a total range of 20–23 caudal rays. If, in regular unstained specimens, one could count only the principal rays, the problem would have an adequate solution; but those rays which are visible include several secondary rays as well as the main rays, and there is no sure way to decide where the main rays end and the others continue. However, in the comparison of counts on my regular specimens with those of the stained specimens, the visible rays usually included the principal rays plus 2–4 secondary rays. The range was as follows: nine had 12 truly visible rays, three had 13, thirty-eight had 14, three had 15, twelve had 16, and one had 18. At best, though, this is a somewhat arbitrary method. Briggs regarded the principal rays in the clingfishes as those that possessed free tips, and these could be counted easily by external examination.

As demonstrated by the stained specimens, all of the fin rays (except in the pelvic fins) have double origins lateral to each other, showing their bilateral origin as modified scales (Mansueti, 1958B:9). In

the fish less than 25 mm the paired rays were separate throughout their length as well as at the base; however, in more mature fish the double rays tended to fuse, except near the bases which remained separate. I found this developmental phenomenon to be true in the pectoral fins as well as in the single fins. One fish also had a doubling of the dorsal and haemal spines on the 26th vertebra. The rays of all fins are unbranched, this observation being confirmed by Briggs (1955:9). There are no spines present in any of the fins except for one bone in the pelvic girdle which may possibly be a highly modified spine of the pelvic fin (Briggs, 1955:9).

Vertebrae and Ribs:—In all seven stained specimens the vertebral count was 27, except for one fish which had only 26 vertebrae. This agrees with Jordan and Evermann (1898:2329) who gave the count for the genus as "about 26" and also falls within the range of 25–32 given by Briggs (1955:89) for the genus. This count includes the last, expanded vertebra (hypural plate) to which the caudal fin rays are attached. The pre-anal (or precaudal) vertebrae numbered 13, a figure which corresponds rather well with the myotome count in the larvae, their pre-anal myotomes numbering 13–15. The balance of caudal vertebrae with haemal spines and the hypural plate numbered 14. Hildebrand and Schroeder (1928: 339) stated that *Gobiesox strumosus* has 12–14 vertebrae. Although they did not say so, they must have meant pre-anal vertebrae, in which case their count agrees with the author's. Note (Fig. 26) that the last anal and dorsal fin rays correspond to the same vertebra.

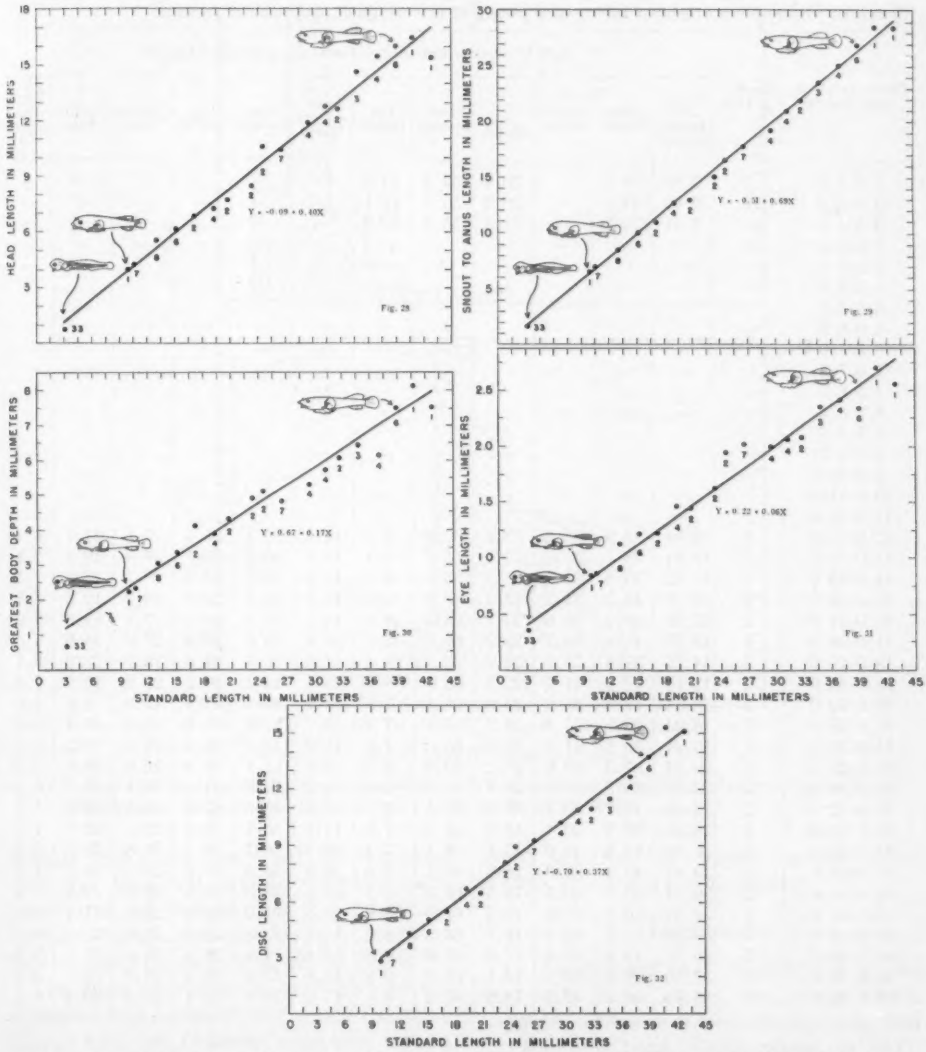
Briggs (1955:9) stated that among the clingfish ribs are absent and are replaced by sessile epipleurals. These may be synonymous with what Romer (1955:179) termed "dorsal ribs." As well as having sessile epipleurals or dorsal ribs, the stained specimens also had intermuscular pleurals, as described by Romer (1955:179), present from the third to the eleventh vertebra (Fig. 26). Generally there were only nine of these on each side, but exceptions were one 20 mm specimen which possessed only eight and one 25 mm specimen which had 10 intermuscular pleurals. The anus is located at the level of the ventral tip of the last pleural.

Teeth:—In the upper jaw of the adult clingfish there are 14–16 teeth on each side, all conical in shape. The more prominent ones in the front number 6–8 and are somewhat irregular in placement and size. Moving laterally and caudad, these are followed by two definite series of four smaller, but regular teeth. Briggs (1955:116) called these recurved canines. There do not appear to be any palatine or vomerine teeth present.

The mandibular teeth number 13 or 14 on each side. Three or four of the most frontal ones are incisors with two or three fairly large conical-shaped teeth following them, termed canines by Briggs (1955:116). In turn, these are followed by two series of three or four regular, smaller conicals. There are also several tiny teeth growing directly behind the main ones. A dental count by Jordan and Evermann (1898:2333) numbered two less on each side for both upper and lower teeth.

Changes in Body Proportions

Generally speaking, the body parts of *Gobiesox strumosus* are quite regular in their growth and consistent in their relationships with each other from larvae to adults. Figs. 28–32 indicate that when the dependent variables of head length, snout-to-anus length, eye length, disc length, and greatest body depth are plotted against standard length, there is a proportional pattern of growth. The only really noticeable variation is in the relative decrease in eye length and increase in head length in relation to the body. In its percentage of standard length the head length doubles itself between the larval and the adult stages (Table 6). Also, the head length gradually increases from one-third to two-thirds of the snout-to-anus length (Table 4). At the same time the diameter of the eye, measured lengthwise, decreases markedly in its proportion to the rest of the body. At 2.85 mm the eye length is one-half of the head length, but by 50 mm it accounts for only one-seventh of the head length. In addition to this change in size, the eye



Figs. 28–32.—Regressions of various body parts on standard length of the clingfish, *Gobiesox strumosus*, fitted by the method of least squares. The numbers below each dot indicate the number of fish in each group of average measurements. The outline drawings are not drawn to scale.

Fig. 28.—Head length on standard length.
Fig. 29.—Snout-to-anus length on standard length.
Fig. 30.—Greatest body depth on standard length.
Fig. 31.—Eye length on standard length.
Fig. 32.—Disc length on standard length.

moves from a lateral position to a somewhat superior position. It is interesting that this adjustment of the sight apparatus fits in so well with the bottom-dwelling habits of the fish. In the adult the forehead has become quite shallow in contrast to its relatively steep slope in the larvae and young. Also the greatest width of the head is no

TABLE 6.—Body proportions of larvae and young of the clingfish, *Gobiesox strumosus*.

Size Intervals in Total Length	Number of Fish	Body Proportions Expressed as Percentage of Standard Length											
		Standard Length in mm	Head Length	Head Width	Greatest Depth	Snout-to-Anus	Eye Length	Interorbital Width	Disc Length	Disc Width	Chin to Disc	Disc to Anus	Anus to Anal Fin
2.5–3.0	3	2.69	20.8	—	20.8	59.5	10.8	—	—	—	—	—	—
3.0–3.5	19	2.96	22.3	—	20.9	56.8	11.1	—	—	—	—	—	—
3.5–4.0	11	3.31	23.3	—	21.8	56.8	10.6	—	—	—	—	—	—
4.0–4.5	—	—	—	—	—	—	—	—	—	—	—	—	—
4.5–5.0	—	—	—	—	—	—	—	—	—	—	—	—	—
5.0–5.5	—	—	—	—	—	—	—	—	—	—	—	—	—
5.5–6.0	—	—	—	—	—	—	—	—	—	—	—	—	—
6.0–6.5	—	—	—	—	—	—	—	—	—	—	—	—	—
6.5–7.0	—	—	—	—	—	—	—	—	—	—	—	—	—
7.0–7.5	—	—	—	—	—	—	—	—	—	—	—	—	—
7.5–8.0	—	—	—	—	—	—	—	—	—	—	—	—	—
8.0–8.5	—	—	—	—	—	—	—	—	—	—	—	—	—
8.5–9.0	—	—	—	—	—	—	—	—	—	—	—	—	—
9.0–9.5	—	—	—	—	—	—	—	—	—	—	—	—	—
9.5–10.0	—	—	—	—	—	—	—	—	—	—	—	—	—
10.0–11.0	—	—	—	—	—	—	—	—	—	—	—	—	—
11.0–12.0	—	—	—	—	—	—	—	—	—	—	—	—	—
12.0–13.0	4	10.04	41.0	36.6	22.5	67.5	8.2	11.1	29.1	25.6	27.5	21.7	6.1
13.0–14.0	3	10.81	39.7	37.3	21.7	65.7	8.1	11.1	30.2	26.1	27.9	19.2	7.3
14.0–15.0	1	11.42	39.3	35.3	21.5	65.1	8.0	10.5	30.3	22.7	28.2	17.7	7.5
15.0–16.0	3	12.37	44.7	38.3	23.4	67.5	8.8	10.5	33.8	30.2	28.2	19.6	5.7
16.0–17.0	2	12.80	41.2	38.6	24.5	66.4	8.8	11.4	31.9	26.6	27.7	19.3	7.9
17.0–18.0	3	13.72	41.4	40.7	22.7	67.3	8.3	10.9	33.6	28.4	27.9	18.8	7.6
18.0–19.0	3	14.79	38.8	39.3	21.2	66.9	8.3	11.2	33.7	27.3	25.7	22.0	6.1
19.0–20.0	2	15.19	41.9	41.9	22.3	65.9	8.0	13.6	34.4	30.2	22.6	15.8	7.4
20.0–22.0	2	16.34	41.8	36.2	23.0	64.1	7.5	11.1	32.3	27.3	12.9	9.8	7.0
22.0–24.0	2	18.02	39.4	41.3	23.2	67.1	7.3	10.7	32.9	29.9	25.4	20.4	6.0
24.0–26.0	3	19.41	36.5	41.6	20.2	66.0	7.5	13.2	35.1	30.8	26.6	19.3	6.7
26.0–28.0	2	20.74	37.0	39.8	21.1	62.8	6.9	11.1	31.1	28.8	26.0	18.1	6.1
28.0–30.0	2	23.33	36.3	39.8	20.9	64.2	6.9	13.5	34.5	31.4	25.1	19.7	6.4
30.0–32.0	2	24.48	43.1	43.1	20.8	67.5	8.0	10.3	36.5	32.6	26.3	20.2	7.0
32.0–34.0	5	26.24	38.3	40.1	18.5	65.8	7.6	11.1	35.7	28.5	26.1	21.1	7.1
34.0–36.0	2	27.19	41.3	40.0	17.1	68.1	7.4	13.1	36.7	30.7	24.8	23.3	5.5
36.0–38.0	4	29.43	40.4	39.0	18.0	65.1	6.8	12.8	34.9	29.5	22.7	18.9	7.3
38.0–40.0	2	30.64	40.6	40.3	18.0	66.7	6.5	12.1	35.0	26.9	23.6	22.8	7.8
40.0–42.0	4	32.31	39.6	38.8	18.5	67.0	6.5	11.5	34.0	28.9	26.8	21.1	6.7
42.0–44.0	2	34.39	41.0	39.1	18.7	68.3	6.5	11.1	32.8	29.1	26.2	22.2	6.7
44.0–46.0	3	36.25	42.2	39.6	17.2	68.0	6.8	12.1	34.4	28.3	27.5	21.6	6.5
46.0–48.0	3	37.65	42.1	40.2	16.1	67.3	6.3	13.8	33.9	29.6	26.0	21.2	6.1
48.0–50.0	3	38.73	39.7	42.1	19.8	67.6	6.1	12.0	34.9	32.1	27.8	20.4	6.2

longer at the opercle but at a point about halfway between the opercle and the orbit. Except for these few shifts, the proportions of the body parts remain fairly much the same throughout growth.

RATE OF GROWTH

The rate of growth of the clingfish is rather difficult to estimate because of its relatively long spawning season and its bottom-dwelling habits. Fig. 33 shows the frequency distribution of clingfish in the months of June and October. The smallest fish found in the October collection of specimens was 18 mm in length. This specimen appeared to be perfectly normal and not stunted in growth. Hildebrand and Schroeder (1928:340) also found a 19 mm specimen as late as October 10. Therefore the spawning season may even extend into

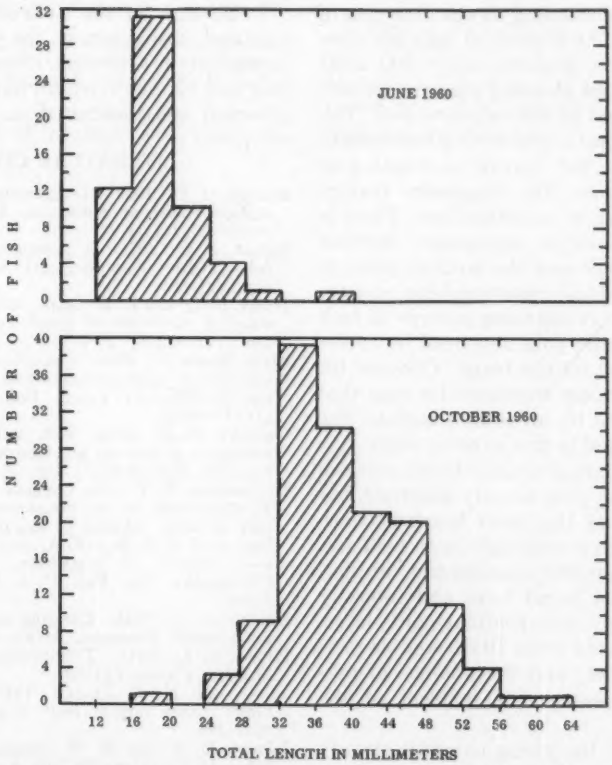


Fig. 33.—Histogram showing a frequency distribution of the clingfish, *Gobiesox strumosus*, at Solomons, Maryland, in the months of June and October, 1960.

August, which Pearson (1941:82) indicated from his plankton samples. Further substantiation of this is that Dr. Mansueti found clingfish embryos at the point of hatching as late as July 22 at Solomons.

The June collection does not give an accurate picture because only young fish were taken, but the October collection was a truly random sample. Disregarding the partly selective factor, the histogram indicates that those individuals in the peak range of size in June, between 16–20 mm, probably reached the peak range of size in October, 32–36 mm. In other words, they grew 16–20 mm over a period of four months, or at least four to five mm per month. However, this rate would not hold true for very young fish when growth is rapid nor for the winter months when growth slows down considerably.

Conclusions

1. Descriptions and illustrations of the egg, early larval stages, and young of the clingfish, *Gobiesox strumosus*, are presented for the first time. Furthermore, development of ossification in the young and the adult is illustrated in detail. Morphometric and meristic data are also provided for 95 specimens ranging from 2.85 mm to 50 mm in total length. The early eggs and larvae of the clingfish are compared briefly with those of ecologically similar species.

2. The eggs of the clingfish, which are laid in empty oyster shells, have an average greater axis of 0.94 mm and lesser axes of

0.67 and 0.79, depending on the direction of measurement. The number of eggs per cluster varies from approximately 300–2500. The numerous oil globules vary in size and are concentrated at the negative pole. The perivitelline space is about 15–20 per cent of the egg volume but narrow or wanting at the negative pole. The diagnostic feature for the early egg is its ovate shape. There is a great difference in appearance between the early embryo and the embryo prior to hatching. The most distinguishing characteristic of the pre-hatching embryo is lack of pigment on the yolk and head but presence of pigment on the trunk. Chances for survival are greatly increased for eggs that are kept aerated by an adult clingfish. The incubation period is five to seven days.

3. Clingfish larvae usually hatch between 3.4–3.8 mm with yolk already absorbed, but in the laboratory they may hatch between 2.8–3.4 mm with a relatively large yolk sac. The most diagnostic combination of features includes a broad head and laterally compressed body with spatulate tail; large, heavily-pigmented eyes; 10–15 stellate melanophore saddles; and the absence of pigment on the posterior 30 percent of the body.

4. By 12 mm the young clingfish already possesses the essential bodily features of the adult. Although its fins have almost attained their full complement of visible rays, the osseous structures of the skull are still somewhat incomplete. Pigmentation has not yet developed into the definitive reticulated patterns of the adult.

5. When it has reached a total length of 40 mm, the young clingfish can properly be considered an adult.

6. Changes in body proportions are generally quite uniform, with slight variation among some individuals. When the dependent variables of head length, snout-to-anus length, eye length, disc length, and greatest body depth are plotted against standard length as the independent variable, it can be observed that the rate of growth in all of these bodily parts is directly proportional to the length of the fish. The head, however, increases while the eye decreases, relative to body growth.

7. Because of the difficulty of hatching eggs and raising larvae, the stages of transformation in *Gobiesox strumosus* between four and 12 mm in length have not yet been observed and illustrated.

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Movements, Reproduction, and Mortality of the White Perch, *Roccus americanus*, in the Patuxent Estuary, Maryland[1]

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ABSTRACT

Over 8,000 white perch were studied in order to understand the population forces of movement, reproduction, and mortality in this representative tributary of Chesapeake Bay. Scales examined in 3,475 fish showed that the maximum ages attained in males and females were 9 and 10 years, respectively. Sizes attained at previous ages were calculated for both sexes, and the means of observed lengths and calculated lengths for corresponding ages compared well. The mean size and weight of males at corresponding ages was less than that of females. The effects of commercial fishing gear that selected out larger fish apparently produced smaller calculated lengths than observed lengths at corresponding early ages. Growth increments for both sexes were greatest during the early years of life. Most males and almost all females enter the commercial and sport fishery at the legal minimum size of 8 inches total length at around age group V. Dominant year-classes were not indicated by the data.

First-year growth of white perch for the 13-year span, 1942–1954, was positively correlated with (a) growth span in the number of days in spring with water temperatures between 10° and 15° C, and (b) with solar radiation in light energy from February to June. It was negatively correlated with: (a) rainfall from February to May; and with (b) an index of population density in the form of commercial haul seine catch in the Patuxent River five years later than the origin of the year-class ($r = -0.753$; $p = <0.01$). The latter relationship suggests that when white perch populations were large in numbers, the individuals from which they arise were usually small-sized; when the populations were small in numbers, the individuals from which they arise were usually large.

The white perch is a schooling, gregarious species, undertaking marked seasonal movements. Of 3,024 tagged and released largely in the river, 324 or 10.7% were recaptured almost entirely within the estuary. The results indicated that the population in the Patuxent is essentially self-contained, and that it can be managed on a local basis in the river. Extensive spring movements were observed from the lower and mid-estuary to upstream tidal fresh water for spawning, indicating the population is semi-anadromous. Summer movements were local and random. Fall movements were minor and usually downstream toward deeper water. In winter white perch remained in deep water and did not migrate until spring. None of the fish tagged outside the river mouth entered the Patuxent; all recaptures came from upper Chesapeake Bay. A meristic study of white perch fin-rays from various zones in the river corroborated the tagging results, indicating that the population is homogeneous. Significantly different subpopulations, based on meristic characters, however, were found between other tributaries and areas in Chesapeake Bay.

A study of gonad development and examination of fish on the spawning grounds showed that female white perch are oviparous and fertilization of eggs is external. They spawned from late March to May in non-tidal and tidal fresh and slightly brackish water areas when water temperatures were between 10° and 15° C. Males matured at a smaller size (50% at 100.3 mm) than females (50% at 105.5 mm standard length). All males in age group II and older, and all females above age group IV, were sexually mature. The early sexual maturity of males partially accounted for the predominance of this sex on the spawning grounds throughout the season.

Mortality rates were calculated from age frequency distributions in the form of catch curves. The annual mortality rate expressed as the annual probability of dying (50%) after age group IV for males was less than that for females (56%). Survival among exploited white perch populations in the Patuxent

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was relatively good when compared to values obtained from unexploited and exploited populations of other fish species. The apparent probability of dying for unexploited white perch under age group V which are subject to death largely by natural causes is slightly less than that for exploited fish above this age subject to death due largely to fishing mortality. A provisional life table was constructed for adult white perch beginning at age group IV, and the mean life expectancy for a cohort after this age was slightly more than 1½ years, indicating that the chance of survival at any age is not very great.

Liberalized management, and its assessment, of the white perch in the estuary is indicated by the population vital statistics. Reduction or removal of size limits on a local basis provide the only positive measure for biological improvement and effective use of the population.

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Introduction

The primary objective of this study was to obtain basic information on the large-scale migrations, local movements, reproduction, age distribution and growth, and mortality of the white perch, *Roccus americanus* (Gmelin), in the Patuxent River, a western shore tributary of the Chesapeake Bay. Certain aspects of the environment were also investigated in order to determine the nature and magnitude of the factors that may have an important effect in determining the relative abundance, rate of growth, and other characteristics of the population. An attempt was also made to obtain information on the ecology of the white perch that would permit prediction of changes in the population density and structure, given certain hydrographic and meteorological data.

The white perch is one of the more common teleost food fishes found along the Atlantic Coast, where it is considered delicate and flavorsome. It rarely exceeds 1½ pounds in weight, and usually attains a length of 9 or 10 inches. It is a semi-anadromous species where it is not landlocked and is distributed along the Atlantic Coast from Nova Scotia to South Carolina [records from more southern waters are questionable (Woolcott, 1955:34)] in coastal marine, estuarine and fresh waters. AuClair (1956:1–60) and Thoits (1958:1–16) have compiled interesting accounts of the species, with emphasis on New England populations. Wherever it is found the white perch has brought about an intensive sport fishery, and in areas where commercial fishing for the species is legal, it is subject to intensive netting. Maryland has led all other states in the commercial harvest of this species (Maryland Tidewater News, 1953:4). The Patuxent River, an important habitat for the species, has been subject to extensive angling (Walker, 1953:1–6), and commercial netting (Table 1).

TABLE 1.—Catch of white perch, *Roccus americanus*, in pounds by various gear in the Patuxent River, Maryland, during the period when the Maryland Fish Management Plan stabilized licenced commercial fishermen and gear, 1944–1955.

Year	Haul seines		Gillnets			Pound Nets[1]	Total	
	Pounds	Percent	Anchor	Drift	Stake		Pounds	Wholesale Value
1944	55,898	77	16	4,150	11,835	300	72,199	$ 4,895
1945	25,084	41	—	86	7,202	2,209	60,662	4,582
1946	57,378	89	100	—	4,223	2,800	64,501	5,932
1947	120,104	65	2,679	3,712	56,827	1,950	185,272	17,272
1948	131,880	86	2,651	3,215	12,446	2,718	152 910	14,081
1949	133,548	90	2,877	600	7,595	3,250	147,870	11,769
1950	86,146	92	—	1,165	3,889	2,475	93,675	7,521
1951	51,979	75	1,400	700	9,386	5,820	69,285	7,096
1952	33,743	71	—	1,015	6,377	6,474	47,609	4,563
1953	68,057	85	—	50	155	—	79,819	9,097
1954	41,343	80	1,075	1,265	7,848	—	51,531	5,287
1955	55,340	74	5,607	—	13,791	—	74,738	7,474
Mean	71,708	77	2,051	1,596	11,797	3,110	91,672	$ 8,297

[1] Includes some fyke net landings for 1948, 1951 and 1952.

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Study Area, Methods, and Materials

Generally, the field work was determined by the season of activity of the fish. Thus in spring months, trap nets were set in various parts of the lower estuary to procure migrating fish for tagging purposes; fish on the spawning areas were tagged in the extreme upper limits of the estuary; and commercial fishermen were contacted in different parts of the estuary to obtain samples for gonad, age, growth and condition studies, and for tag recaptures. In all cases random samples of the captured fish were examined in order to get a representative sample for determining sex ratio and age and size composition. Plankton nets were set or hauled over certain areas to determine the location of spawning beds through discovering the presence of eggs and prolarvae. In the upper spawning area, where most conventional trap nets could not be used, bank dip nets and bow nets were utilized to procure fish for tagging. During summer, angling catches were sampled, and commercial fishermen were further contacted for fish. Small haul or beach seines were used and a limited amount of small-scale trawling operations were carried out to obtain young-of-the-year fish to determine their distribution in various parts of the estuary and the distribution of sizes in relation to depth.

Descriptions of the area:—The study was concentrated in the tidal waters of the Patuxent River estuary. An earlier study by Mansueti (1950:131, 279), of the ichthyofauna of the Patuxent River watershed, indicated that the white perch was restricted to the lower 50 miles. Additional surveys in the waters above the upper limit of this general demarcation corroborated this fact. The Patuxent, situated entirely in Maryland, has its headwaters in north-central Maryland at an altitude of about 800 feet in Howard and Montgomery Counties. It pursues a general southeasterly course, and empties into Chesapeake Bay about 25 miles north of the mouth of the Potomac. Its length, including the upper watershed measured on a straight line, is approximately 80 miles, and its drainage area is 963 square miles, according to the Chief of Engineers, United States Army (1930:1–142). There are no natural lakes or impoundments in the Patuxent drainage system, except a few coastal, barrier beach ponds at the mouth (Mansueti, 1954:65). Tridelphia Reservoir, completed near Olney in 1944, and Rocky Gorge Reservoir, completed near Laurel in 1954, are the only large artificial lakes in the watershed. Regulation of flow at the dams have an important effect on the water level and fluvial characteristics on the river below.

The lower 35 miles of the estuary ranges in width from 0.2 of a mile to 2 miles. Tidewater extends upstream to Hardesty, about 56 miles above the mouth. The range of tide varies from 1.2 feet at the Patuxent River mouth to 2.5 feet at Nottingham, about 40 miles above the mouth. At Hardesty, the tidal range reaches a maximum of about one foot during the low stages of fluvial flow. About 63 miles above the mouth at Priests Bridge, a number of large tributaries flow into the main branch of the Patuxent. Above tidewater the river is narrow and shallow with widths between banks of 50 to 150 feet. At low stages, the mean depths are from one to two feet, except in pools and channels where greater depths occur. Freshets are of almost annual occurrence, although extreme heights are rarely attained. At Queen Annes Bridge near Hardesty, where an important spawning area is located, heights of flood water of 10 to 12 feet are occasionally reached. Such excessive flows are now controlled by the spillway manipulation at the two reservoirs cited above.

General ecological zones:—The tidal portion

of the Patuxent River was arbitrarily divided into six zones for the purposes of this study. A seventh zone is indicated immediately outside the river mouth in Chesapeake Bay (Fig. 1 and Table 2). These zones were characterized by salinity ranges taken from Nash (1947:148–58) and fluvial and topographic characteristics (Fig. 1) based on observations of the vegetation types; nature of bottom and gradient, and other obvious features encountered early in the study. The study area of Nash coincided very closely to that selected for the white perch investigation. Salinity records taken during the study in the vicinity of Nash's stations fell well within the ranges given by him. There exists in the lower quarter of the river a deep channel ranging in depth from 30 to 115 feet, which, except for an increase in depth a few miles inside the mouth of the estuary, generally decreases upstream. In the upper half of the estuary the channel varies in depth from 10 to 46 feet. The bottom of the estuary is generally muddy, the depth of the mud decreasing upstream, except in the upper middle regions where it is sandy, as generally are the shores. The latter are marshy and muddy at the head of tidewater. Due to the gradual narrowing and reduction in depth of the estuary upstream, the current velocity increases in this direction from about 0.9 feet per second at full strength in the estuary mouth to about 1.6 feet per second near its upper limits. At each end of the estuary there is little difference between flood and ebb strength velocity, but, throughout the greater part of the estuary, surface flood strength velocity exceeds ebb strength velocity by about 0.7 feet per second, according to Haight, Finnegan and Anderson (1930:1–143). It is important to note also that the lower Patuxent River is a typical two-layered estuary, in that there is a net upstream movement of subsurface high saline waters and a net downstream movement of fresher, less dense, surface waters with each tidal cycle (Pritchard, 1951:375).

Measurements:—Standard and total lengths were recorded for each fish as outlined by Hubbs and Lagler (1949:13). Both measurements were useful in obtaining a reliable figure or conversion factor for the ratio between the standard and total length. Conversion factors from standard to total lengths were necessary in the discussion concerning gear selectivity and the minimal legal size in total length. The ratios, total length to standard length and vice versa, are shown in Table 3 for male and female fish from two localities. Every effort was made to avoid a digit bias in which a tendency to favor certain digits was possible among certain observers, as has been described by Sette (1941:77–80). Weights of fish were recorded by conventional methods. Scale samples for age and growth studies, and other data on sex and breeding condition, and general condition, were taken for each fish, together with prevailing ecological and hydrographic conditions at each locality.

Some of the fish (N = 100) that were marked and preserved in 10 per cent formalin for morphometric and gonad study and for dissection were weighed and measured while still fresh in March, 1953. Since most of the preserved specimens—many of which were not weighed and measured in the field—constituted a part of the material used for the study of growth, it was of some importance to know the extent of shrinkage in length and added weight brought about by formalin. They were reweighed and remeasured on July 10, and September 20, 1952 by the same method as the fresh specimens and by the present investigator. The ratio between preserved length and fresh length was determined and the value 1.021 was used to correct for shrinkage after preservation. A slight increase in mean weight occurred after preservation, and the correction factor 0.993 was used to convert preserved to fresh values.

Tagging:—The selection of a proper tag for the white perch depended on the following points: (a) the length of time that a tag is to remain affixed to a fish; (b) personnel available for tagging; (c) whether trained or untrained personnel will make recaptures; and (d) methods of capturing and handling a marked fish. A review of the variety of tags cited in Rounsefell and Kask (1945:320–63), Calhoun, et al (1951:301–14), and Calhoun (1953:200–18), indicated that the Petersen plastic disk tags would be the best suited for this study since they would be retained at least a year, on the average, by various fish species. Stroud (1953:274) used a jaw-tag on white perch in Massachusetts, but the decision against its use on Maryland fish was based on its somewhat more complex attachment procedure. Those used were about 11 mm in diameter and 0.5 mm in thickness, with a center hole about 1.0 mm in diameter. One was yellow (marked "Return both disks", a number and "C.B.L."—for Chesapeake Biological Laboratory) and the other red (marked with "Chesapeake Biological Laboratory, Solomons, Maryland, return both disks, help appreciated."), were attached to the fish by means of a straight nickel-alloy pin inserted directly into the flesh below and between the first and second dorsal fins. This location for tag insertion was determined by a body site scale sampling study for age and growth purposes (Mansueti, 1960:108–9). After a scale sample was taken, the pin insertion was facilitated by the area free from scales.

During the four years of tagging with Petersen disks, 3024 white perch were released in the Patuxent River, except for a few released in Chesapeake Bay near the mouth of the River. Most of the tagging effort was expended during the spring months of 1953 in the upper and lower parts of the river. Although an attempt was made to tag fish in each of the zones during the four seasons of the year, this action was made impossible by the seasonal variations in commercial fishing, by the lack of suitable sites for trapping, by the non-availability of white perch to the methods used in capturing the fish, and by similar obstacles. Table 4 shows the over-all seasonal tagging results, with numbers of fish recaptured in relation to those tagged by zone and month of release for the four-year period.

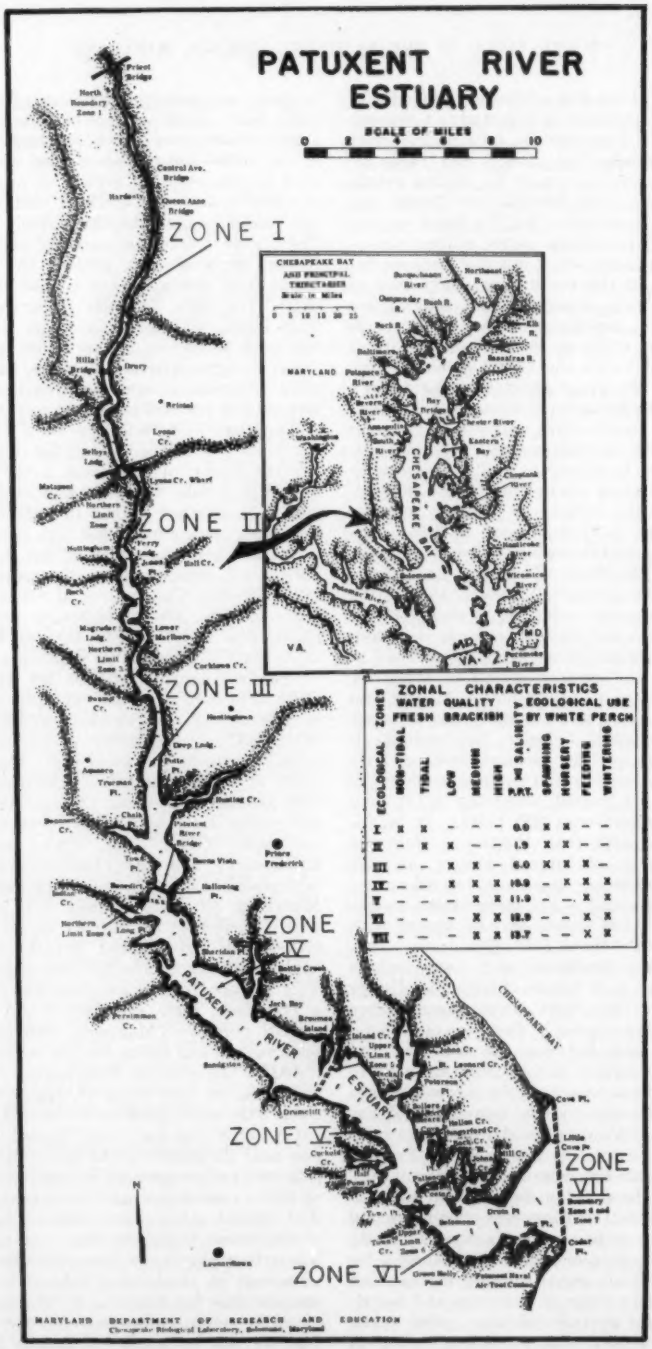

Fig. 1.—Patuxent River estuary, Maryland, showing general ecological zones, collecting localities, and locations of tag returns of white perch, *Roccus americanus*. The inset of the Maryland portion of Chesapeake Bay shows the general location of the Patuxent tributary in relation to the upper part of the Chesapeake system. Relative salinity values in the various zones are as follows: low—1–8 ppt; medium—3–12 ppt; and high—6–15 ppt. See Table 2 for degree of overlap of brackish water.

TABLE 2. General characteristics of the ecological zones in which the Patuxent River was divided during the population study of white perch, *Roccus americanus*.

Zones	I	II	III	IV	V	VI	VII
Length in miles	16	8	11	13	8	8	—
Boundaries							
North	Priests Bridge	Lyons Creek	Magruder Lndg	Long Point	Drumcliff	Thomas Point	Chesapeake Bay; outside Patuxent R.
South	Selbys Lndg	Lower Marlboro	Patuxent R. Bridge	Broomes Island	Point Patience	Cove Point	
Adjacent land	Swamps, Woods	Marshes, Woods	Farms, Woods	Farms, Woods	Farms, Woods	Farms, Woods	High bluffs
River (Mean values, = ℞)							
Width (℞ ft.)	70	1000	1800	2400	6000	10,000	Variable
Depth (℞ ft.)	4	8	15	20	30	36	40
Flow	Steady	Moderate	Slow	Slow	Slow	Tidal	Tidal
Surface salinity							
Upper limit	0.0	0.0	2.2	6.3	7.5	8.4	8.8
Lower limit	0.0	4.5	12.9	15.2	16.7	20.4	18.4
Mean (℞)	0.0	1.9	6.0	10.9	11.9	12.9	13.7
Tidewater type							
Fresh	x	x	x	—	—	—	—
Brackish	—	x	x	x	x	x	x
Salt	—	—	—	—	—	x	x
Ecol. use by white perch							
Spawning	x	x	x[1]	—	—	—	—
Nursery	x	x	x	x	—	—	—
Feeding	—	x	x	x	x	x	x
Wintering	—	—	—	x	x	x	x

[1] Only upper part.

Most of the white perch used in the tagging experiments were captured alive by experimental gear in the form of small pound-like trap-nets, fyke nets, bank dip nets, bownets, small haul seines, and other gear as listed in Table 5. The nature and degree of selectivity for size and sex of fish by such gear are also indicated. Certain fish whose sex could not be determined are listed under various tables under "??." Some of the samples for tagging were procured by commercial fishermen in the course of fishing operations and by hook and line. In all cases the fish were taken directly from the nets and either held in a live box or placed in a large tub for immediate tagging. All fish were carefully inspected for injuries and only apparently unharmed, vigorous individuals were tagged. Fishes tagged from commercial catches were selected as randomly as possible. Usually the tagging was done by one man who held the fish in the left hand and applied the tag with the other. After affixing the tags, the fish were released gently by placing them head-first into the water.

Commercial fishermen accounted for most of the recovered tagged fish, although many were caught and returned by sport fishermen (Table 6). To encourage interest in the tagging program, large placards were placed near the communities or the sites where tagging was conducted. A reward of 50¢ was offered for the return of tagged fish with complete information on time and place of capture. During much of the program, trips were made to the fishing areas and both fishermen and dealers were contacted to obtain recaptured fish. Since there is a great diversity of landing areas for the fish and since fishing is spread over a large number of people engaged in licensed and unlicensed commercial fishing, as well as sport fishing, there is reason to suspect that not all potential takers of tagged fish were contacted. In addition, a few people are reported to have refrained, for various reasons, from turning in tags that they possessed.

TABLE 3. Correction factors for converting total to standard, and standard to total length for white perch, *Roccus americanus*, taken from two zones in the Patuxent River.

Sex	Sample source zone	Number of fish	Mean standard length (S.L.)	Total length (T.L.)	T.L. to S.L.	S.L. to T.L.
Male	I	78	5.10	6.35	0.80	1.24
	V	78	6.08	7.52	0.81	1.24
Female	I	78	5.67	6.98	0.81	1.23
	V	78	6.84	8.33	0.82	1.22

Meristic characters:—Preliminary analysis of meristic features in the white perch indicated that dorsal, anal and pectoral fins, individually, and collectively summed to form the "character index," as used by Raney and de Sylva (1953:405–509), and Raney, et al (1954:376–96), would serve as useful indicators of discrete subpopulations. Counts of the number of rays in these fins exhibited the most pronounced regional variations of all morphological features examined.

Great care was exercised in the collection of the sample intended for use in distinguishing between local populations of fish. The samples were restricted to young-of-the-year fish. Since all the potential white perch spawning areas, where pure samples of a population presumably would occur, were unknown in the Patuxent River, collections were made during the season of least movement. The short mean range of movement during the summer and autumn months indicated that if local populations existed along the estuary, there

TABLE 4. Tag returns of white perch, *Roccus americanus*, compared with the numbers of tagged fish released in the Patuxent River, shown by zone and by month of release, 1952–1955.

Month	Tagged sample[1]	Zones							Total	Per-cent recaptured
		I	II	III	IV	V	VI	VII		
Feb.	Released	—	—	—	—	—	—	24	24	
	Recaptured	—	—	—	—	—	—	2	2	8.3
Mar.	Released	—	—	—	—	—	48	—	48	
	Recaptured	—	—	—	—	—	10	—	10	20.8
Apr.	Released	996	50	—	—	392	—	—	1438	
	Recaptured	161	3	—	—	69	—	—	233	16.2
May	Released	711	—	—	—	308	—	—	1019	
	Recaptured	28	—	—	—	18	—	—	46	4.5
June	Released	—	—	—	—	—	47	—	47	
	Recaptured	—	—	—	—	—	4	—	4	8.5
July	Released	—	7	2	94	57	107	—	267	
	Recaptured	—	—	—	3	4	5	—	12	4.5
Aug.	Released	—	9	23	—	19	—	—	51	
	Recaptured	—	—	1	—	3	—	—	4	7.8
Sept.	Released	—	—	—	—	—	—	—	—	
	Recaptured	—	—	—	—	—	—	—	—	—
Oct.	Released	—	—	—	—	—	43	—	43	
	Recaptured	—	—	—	—	—	—	—	—	—
Nov.	Released	—	—	87	—	—	—	—	87	
	Recaptured	—	—	13	—	—	—	—	13	14.9
Total	Released	1707	66	112	94	776	245	24	3024	
	Recaptured	189	3	14	3	94	19	2	324	10.7
Per-cent Recaptured		11.1	4.5	12.5	3.2	12.1	7.8	8.3	10.7	

[1] Samples of recaptured fish were taken at any time after the month of tagging; tagged fish were released only during the designated month. Some tags were returned subsequent to this compilation, but they do not appreciably alter the general pattern above.

would be a minimum of mixing during this season. All the samples were restricted to fish collected largely by beach seines during those seasons at various stations from Zone I to Zone VI. Specimens taken in other parts of Chesapeake Bay were collected in fall months during the same year.

Counts of the dorsal, anal, and the left pectoral fin were enumerated according to recommendations of Hubbs and Lagler (1947:10). The last two fin-ray bases in both the dorsal and anal fins were counted as one. All the rays, including the rudiments, were counted in the pectoral fin. Counts were repeated to insure perfect agreement in the results from the study of each fin before the accumulation of the body of data upon which this part of the report is based. Certain groups of fish were counted twice, and less than five per cent of the samples showed disagreements. Discrepancies in the number of specimens used in the counts are due to mutilated or otherwise uncountable fins. Such incomplete counts were discarded.

Gear selection:—At least 14 methods of collection were used to sample white perch populations in the Patuxent River estuary (Table 5). The sampling problem presented by the selective action of various gear in the collection of materials for scientific investigations, particularly in growth computations, has been known for about five decades. Royce (1957:25) has discussed some of these difficulties. If a gear selectively takes mostly larger and older fish, without equal representation of the smaller and younger fish, it is clear that a distorted picture of the age and sex structure of the population will be obtained. A slight change in the mesh size of gillnets, for example, can affect the size and age composition of catches as has been shown by Hile (1936:294–306). From a biological viewpoint, gear selection tends to bring about a great reduction in numbers of fish in that portion of the population most susceptible to capture by a standard commercial gear. Obviously, the withdrawal of large quantities of commercial-sized fish produces an abnormal condition in size, age, and sex distribution of the population as a whole. The white perch study, on the one hand, was considerably enhanced by representative samples from many types of gear so that a large and varied collection was available for study. On the other hand, it was complicated by the different weight that the samples taken by various gear and methods exert on the population attributes that are computed.

Aging by scale analysis:—The method of deciphering the age of fishes by counting rings or annuli on the scales has been used on many species and by a great many workers (Van Oosten, 1929:265–428; and Hile, 1941:189–337). The annuli on the white perch scales were counted to determine age in this study (Fig. 2). The validity of the annulus as a true year-mark has been proven for many species of fish, but, although several age and growth studies have been presented for the white perch, a critical study of the application of the scale method to this species has never been undertaken.

Data were collected from 2189 females and 2146 males, which with some fish of unknown sex, totalled 5440 fish. Scale samples were taken in the field from all specimens except those preserved for morphometric and gonad studies in formalin. The latter group of fish were processed in the laboratory. The collection of samples was complicated by gear selectivity, differential availability of certain sizes, and variable distribution of sexes and ages of fish during the various seasons. An attempt was made to increase the precision of the estimates of the parameters by taking each sample so that all individuals in the population had an equal chance for inclusion by the use of random number tables. The scale samples, consisting of 10 to 20 scales, were removed and were stored in standard coin envelopes (2¼″ x 3½″) on which were recorded species, length.

TABLE 5. Gear and other sampling methods used to collect white perch, *Roccus americanus*, within the Patuxent River estuary.

Method or gear	Season fished	Zones where fished	Depth fished	General habitat type fished	Stretched mesh size of nets	Selectivity of gear or method
			feet		*inches*	
Experimental explosions U. S. Navy	All year	V to VII	0–120	Deep waters	—	No selectivity known except no young fish taken. Selective for large fish; however, found in deep water.
Hook and line	All year. Rarely in winter	III to VII	0–90	Shoals deep water in river and creeks	—	Most large fish over the legal minimum limit of 8″.
Small bag haul seine (30–50′)	All year. Except winter	I to VII	<5	Shoals of rivers and creeks	½″	No selectivity of fish found in shoal waters; mostly small fish.
Commercial haul seines (up to 1800′)	All year. Rarely in winter	II to VI	<10	Shoals of river and creeks	Legal minimum 2½″	Selective for large fish; most fish over legal minimum limit of 8″.
Commercial stake gillnet (up to 3000′)	All year. Rarely in summer	II to V, VII	<15	Shoals of river and creeks	Legal minimum 2½″	Selective for large fish; most fish over legal minimum limit of 8″.
Commercial anchor gillnet (up to 3000′)	Winter and spring	II to V, VII	<30	Deeper waters of river and large creeks	Legal minimum 2½″	Selective for large fish; most fish over legal minimum limit of 8″.
Commercial drift gillnet (up to 3000′)	Winter and spring	II to III, VII	20–30	Deep water without snags	Legal minimum 2½″	Selective for large fish; most fish over legal minimum limit of 8″.
Experimental anchor gillnet (up too 500′)	Winter and spring	II to IV	<30	Deep waters	1½″	Selective for medium-sized fish.
Commercial pound or live trap net	All year. Mostly fall	III to VI, VII	<12	Shoals	Legal minimum 2¼″	Selective for large fish; most fish over legal minimum limit of 8″.
Experimental small pound-like trap net	Spring and summer	IV to VI	<12	Shoals of river and creeks	1½″	Selective for medium-sized and large fish.
Experimental fyke or hoop net	Mostly in spring	IV to VI	<20	Shoals to deep waters	Same as above	Selective for medium-sized and large fish.
Midstream bownets	Spring only	I	<6	Shoal water on spawning grounds	Legal minimum 2½″	Selective for large fish; most fish over legal minimum limit of 8″.
Bank dip net	Spring only	I	<6	Shoal water on spawning grounds	Wire 1″ diameter	Selective for medium-sized and large fish; few fish are over legal minimum limit of 8″.
Small experimental trawl	Summer, fall and winter	IV to VII	<40	Deep water	½″	Selective for small fish, although catch was too poor for a reliable judgment.

weight, sex, state of gonads, county, locality, date, gear remarks, tag numbers (if applicable), time of tagging, and name of investigator. Thus each envelope contained the history of each specimen used in the study, and the information for each day's catch was catalogued in notebooks.

After scales were removed from a fish, they were left to dry in the scale envelopes until mounted on slides. At least four scales from each fish were mounted and an impression of the sculptured surface of the scale was made on a lumerith cellulose acetate slide by means of a scale press originally designed and described by Nesbit (1934:373–6). This method had an important advantage in that thick, relatively opaque and typically ctenoid scales through which transmission of light is impaired could be read for age since the sculpturing of the scale and the occurrence of annuli were discernible on the impression. Regenerated and abnormal or irregularly shaped scales were not mounted, although in instances involving small scales, regenerated areas could not be discerned until after the impressions were made. The scale impressions to be studied were magnified 23 times by means of a Rayoscope Projector.

Scales were viewed for detailed structures of the circuli, radii and annuli. Other details concerning the nature of the white perch scales may be found in Cooper (1941:133) and the study dealing with scales from different parts of the body showing that scales are variably shaped,

TABLE 6. Recaptures by various gear and methods of fishing of tagged white perch, *Roccus americanus*, by sex and by zone in the Patuxent River estuary, 1952–1955.

Method of collection	Sex[1]	Zone of tag recovery							Totals	Grand total	Per-cent recaptured
		I	II	III	IV	V	VI	VII			
Haul seines	FF	—	—	18	11	22	—	—	51		
	MM	—	—	17	8	8	1	—	34		
	??	—	—	1	—	2	—	—	3	88	27.2
Gillnet type unknown	FF	—	3	13	2	8	2	1	29		
	MM	—	2	16	—	4	—	—	22		
	??	—	—	8	1	1	—	—	10	61	18.8
Bank dip nets	FF	16	—	—	—	—	—	—	16		
	MM	36	—	—	—	—	—	—	36		
	??	—	—	—	—	—	—	—	—	52	16.0
Bow net	FF	15	—	—	—	—	—	—	15		
	MM	22	—	—	—	—	—	—	22		
	??	—	—	—	—	—	—	—	—	37	11.4
Hook and line	FF	—	—	3	2	5	1	—	11		
	MM	1	—	2	3	1	1	—	8		
	??	—	—	—	—	3	3	—	6	25	7.7
Fyke nets	FF	—	1	8	1	—	1	—	11		
	MM	—	—	6	—	—	2	—	8		
	??	—	—	—	—	—	1	—	1	20	6.2
Stake gillnets	FF	—	—	5	—	2	—	—	7		
	MM	—	1	3	—	—	—	1	5		
	??	—	—	—	2	—	—	—	2	14	4.3
Miscellaneous[2]	FF	2	1	4	2	2	—	2	13		
	MM	1	2	6	1	1	2	—	13		
	??	—	—	—	—	—	—	1	1	27	8.3
Totals		93	10	110	33	59	14	5		324	99.9

[1] FF = females; MM = males; and ?? = unsexed fish.

[2] Miscellaneous consists of methods of recapture and numbers of fish: (a) Unknown—12; (b) Pound nets—7; (c) Found dead—4; (d) Anchor gillnets—2; and (e) Pound-like trap nets—2.

depending on the source (Mansueti, 1960:107). It is the intention of this paper to demonstrate that these scars are yearly in occurrence and hence can be used to determine the age of white perch.

Among white perch, age analysis on scales was facilitated by a number of peculiarities that could be readily recognized only after some experience. "Cutting over" or "crossing over," of the annulus, which was of great diagnostic value, could be recognized when scale development had ceased and the outer ridges or circuli tended to flare outward or end abruptly on the side of the scale (Fig. 2B). The presence of discontinuous circuli, and crowding of the circuli prior to resumption of growth, also aided in annulus detection. The erosion or resorption of portions of scales of some of the older fish rendered peripheral annuli difficult to determine. In general, however, using criteria set forth by Cooper (1941:133–4), and many other fishery biologists studying fish with ctenoid scales, very little difficulty was encountered in aging the vast majority of scales.

Fish whose scales are without annuli, that is, fish in the first year of life, are designated as members of the 0-age group. The ages of the older fish are expressed by Roman numerals corresponding to the number of annuli or completed years of life. A fish in its second year or summer of life (with one annulus) is a member of age group I (roughly 12 months after hatching); third year or summer of life (with two annuli)—age group II; fourth year or summer of life (with three annuli)—age group III; etc. Fish taken in winter when growth had ceased or early spring before annulus formation, however, are advanced one year; thus, a two-ring fish during this period was classified as age group III, a three-ring fish as age group IV, etc. White perch hatched in the same calendar year are members of the same year class or brood regardless of their age at capture. For example, the 1950 V age group, the 1951 VI age group, and the 1953 VII age group are all the 1945 year class fish.

Bias in aging:—Biased (reader faults) and unbiased (scale faults) errors could and did exist in the scale mark interpretations of white perch. Reader faults occur when a reader mistakenly omits a clear ring or annulus, or through carelessness or acquired bias, tends to choose as valid rings, certain marks that have been determined as false annuli by other scale readers. Scale faults are due to inherent qualities of the scale such as failure to show an annulus due to abnormal conditions of food and temperature, and other factors that affect growth, or production by these growth factors of a false mark on all scales of a fish, which cannot be distinguished from a true annulus. False annuli, so-called "spawning marks" and other accessory checks, which cause so much difficulty in the interpretation of the scale structure of some fish, were of infrequent occurrence in the white perch scales from the Patuxent River. Such marks were found in fish that ranged from two to five years old, rarely older, and were conspicuous by their close proximity to an annulus. Since the formation of the annulus did not occur until after the spawning season, it was assumed that such accessory checks preceded the true annulus. Tentatively, these checks were identified as spawning marks. Among a few fish in which an accessory check could not be so assigned the sample was discarded because of the inability to decide whether certain checks were actually yearmarks. Regenerated scales, in which the clear, well-defined focus is replaced by an expanded central area, is devoid of circuli and annuli, and exhibits a rough or granular appearance and irregular outline, were always discarded.

Reader bias in annulus detection was studied by having a series of white perch scales read independently by three people. At the first scale reading session major differences in interpretation were verbally analyzed and more definite criteria were established. Table 7 lists the percentage of

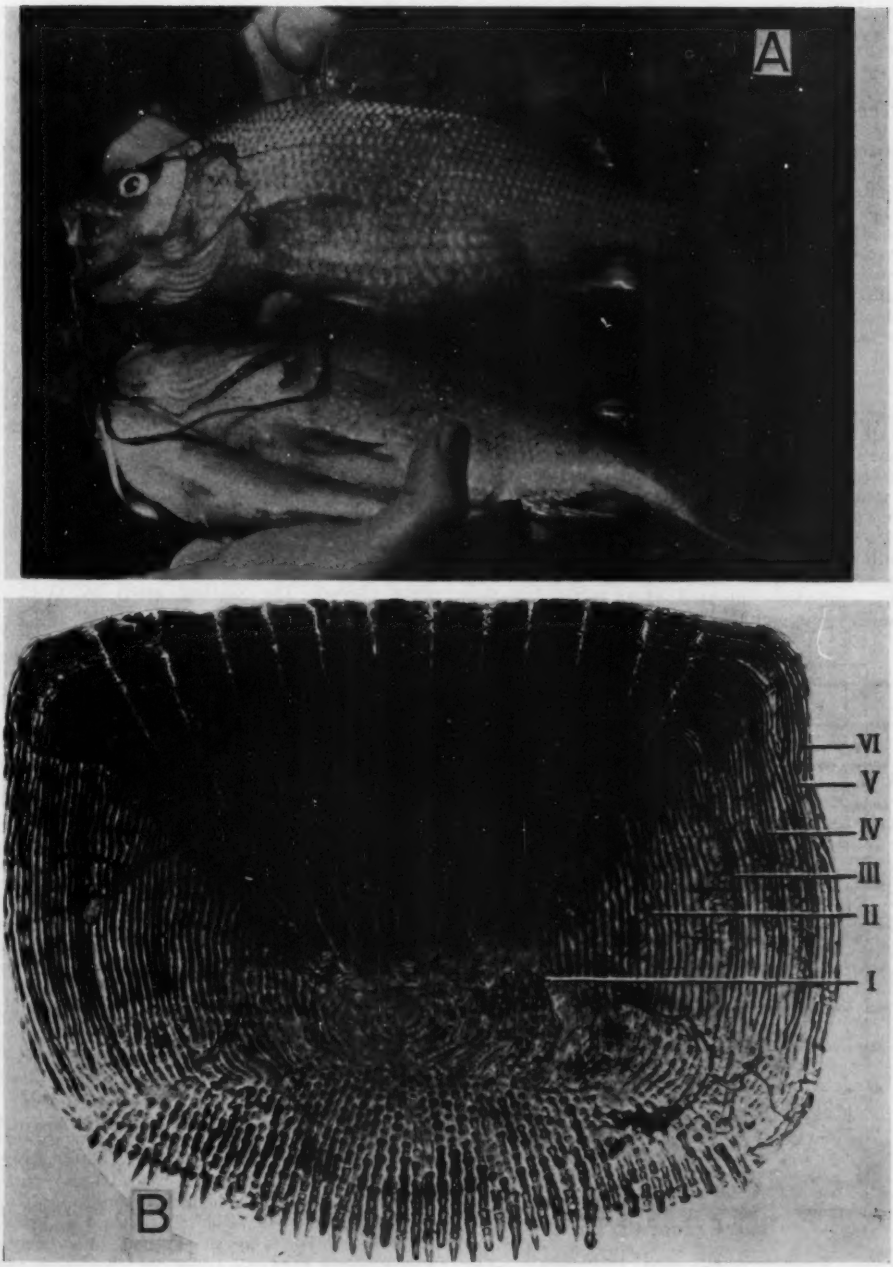

Fig. 2.—The white perch, *Roccus americanus*, and an example of its scale: (A) a pair of gravid females in age group VII taken on the upper Patuxent River spawning grounds in April, 1953; and (B) scale of a six-year-old female, 196 mm S.L. (9½ inches T.L.), showing cutting over and other characteristics of annulus detection.

TABLE 7. Disagreements on assigning age to scales of the white perch, *Roccus americanus*.

Group	When viewed	Size group total length	Number of fish	Percentage disagreement	
				First trial	Second trial
A	July, 1952	Less than 180 mm	50	7	4
B	July, 1952	More than 180 mm	50	12	6
C	August, 1952	Less than 180 mm	50	4	2
D	August, 1952	More than 180 mm	50	8	4
E	February, 1953	Range 130-250 mm	75	11	5

disagreements between this investigator and other scale readers on white perch scales from large and small fish read on three different occasions. As can be seen, when the second readings were compared with the first readings, there is a definite improvement on the second reading. It can also be seen that scales from younger fish can be aged with greater certainty than the older fish. The inconsistencies, no more than one year off from the estimates, indicated that a few occurred among four and five year old fish, a few more between five and six, and most of them in ages above six years old. While these figures do not prove the complete validity of age readings, they do assure that the annuli on white perch scales can be counted with a good degree of consistency and precision.

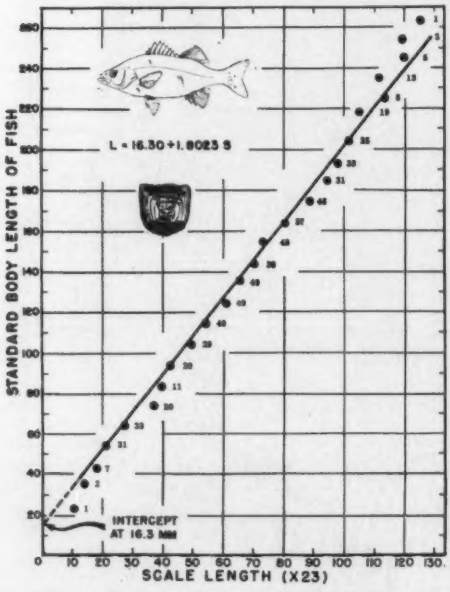

Fig. 3.—Scale-length and body-length relationship of the white perch, *Roccus americanus*, both sexes combined. The number of specimens for each mean value is given next to black dot.

Scale-length/body-length relationship:—Most published studies dealing with the method of calculating body lengths of white perch at younger ages from the scales of a fish assumed that a direct proportion existed between the scale and body growth throughout the entire life. The present investigation, based on random samples of 626 white perch of both sexes from the entire estuary, shows that this phenomenon is not exactly true. Thus, the scale-length/body-length relationship for purposes of introducing a correction factor in back-calculating growth rates of white perch was determined. Everhart (1950:273–4) demonstrated that since there is no evidence to suggest that taking a key scale, or using scales from the area where they first arise, gives an added precision in predicting previous lengths, the practice of basing a scale-length/body-length relationship in white perch on key scales was omitted. Scale-lengths corresponding to body-lengths for individual fish based on random samples of both sexes for all lengths of white perch were plotted. The method given by Goulden (1939:58–61) was used, in which a large series of paired values could be summarized in a frequency distribution table of the two variables. The means of body lengths from the various scale length groups for both sexes combined were plotted as points in Fig. 3.

The relationship between scale-length and body-length can be expressed by the equation for a straight line: $L = c + a\,S$, where L = body-length, S = scale-length, c and a are constants. Since the purpose of the work is to calculate intermediate values of L for known intermediate values of S, the required regression equation is that which provides an estimate of L in terms of S. This has been found to be $L = 16.30 + 1.80\,S$. Fig. 3 shows, and the equation indicates, that the scale-lengths and fish-lengths are not in direct proportion, although their increments are. The formula for the back calculation of body lengths, if a direct proportion between the scale and body growth is assumed, is:

$$\frac{\text{Length of scale radius to annulus} \times (S')}{\text{Length of total scale annulus } (S)} = \frac{\text{Length of fish when annulus x was formed } (L')}{\text{Length of fish at time scale sample was obtained } (L)}$$

$$\text{or } L' = \frac{S'}{S} L$$

Intermediate values of L can be adjusted or corrected with little difficulty, assuming that a constant relationship exists between the two variables. Lee (1920:22) pointed out that any intermediate

fish-length may be calculated where the above type of relation applies by means of the formula:

$$L' = c + S'/S(L - c)$$

If the scale-length/body-length relationship in the present case applied over the whole life of the fish, it would follow that the scales were formed when the white perch were of mean standard length of 16.3 mm (16.7 mm total length), i.e., equal to the constant c in the equation above, which represents the intercept of the extrapolated regression line upon the L axis. The general validity of this assumption was verified in an examination of two collections of very small white perch (20 specimens, ranging in standard length 9.6 to 14.5 mm collected May 21, 1953 in a plankton net two miles north of Lower Marlboro in the Patuxent River; and 11 specimens, ranging from 20.5 to 27.7 mm S.L. collected in small mesh seine June 12, 1954, at Hallowing Point, Patuxent River). None of the first small-sized group possessed scales after careful microscopic examination, whereas all of the somewhat larger second group possessed well-defined scales. AuClair (1956:28) found specimens 1.6 inches T.L. with a few circuli on their scales. The scales in the latter group ranged from 0.40–0.55 mm in diameter, and possessed from 4 to 6 well-defined circuli. Thus it appears that scales appear first among white perch juveniles somewhere between 15 and 20 mm standard length, although the extrapolation of the regression line through the standard length axis is an artificial value as suggested for the striped bass (Mansueti, 1961:12). AuClair (1956:28) plotted body and scale lengths for some young-of-the-year white perch from Maine and concluded that scales were formed at 0.9 inches (T.L. = 22.8 mm. T.L. and 18.5 S.L.), which is close to the Patuxent estimate. Saila and Horton (1957:30) computed a body-scale correction factor of 28 mm T.L. (= to about 22.7 mm S.L.) for 226 landlocked white perch in Rhode Island. Their value is about 28 per cent higher than that for the Patuxent sample, but the difference is probably of no great importance. In the Patuxent sample the regression equation for 306 male white perch was $L = 16.42 + 1.79\ S$ and the 320 females was $L = 17.93 + 1.80\ S$. A test of significance of the differences between regression coefficients for the sexes indicted that there was no statistical difference. For this reason the correction for both sexes combined was used in the back-calculations (Fig. 3).

Alinement charts or nomographs were used in actual practice to calculate the growth of fish from scale measurements, based on rapid and simple applications suggested by Carlander and Smith (1944:157–62). The use of the nomograph involved only the horizontal rulings in millimeter units of the paper. The locations of the focus, the several annuli, and the edge of the projected image of a scale were marked on a strip of yellow paper. The straight edge of the strip was then placed on the nomograph in such a position that the mark corresponding to the focus of the scale was on the "zero" line (in actual practice at 16.3 mm). The mark corresponding to the edge of the scale was on the line representing the length of the fish at capture. The lengths of the fish at the time of each annulus formation was then read directly from the nomograph at the points where the annuli were marked on the strip. Comparisons with the calculations based on substitutions of the equation revealed that the nomograph gave accurate results.

Differences in growth calculated by body-scale correction and direct proportion:—A comparison of the growth histories of eight and nine age groups of male and female white perch, respectively, as calculated by the direct proportion and from the body-scale correction method provides a measure of the error involved in the former method. Table 8 for females shows that the ex-

TABLE 8. Comparison of the growth histories of nine age groups of female white perch, *Roccus americanus*, captured in the Patuxent River as computed from scale measurements by the direct proportion (uncorrected lengths) and by a body-scale (corrected) method.

Age group	Lengths[2]	Calculated standard length in mm at end of year of life									
		1	2	3	4	5	6	7	8	9	10
I	C	61	145[1]	—	—	—	—	—	—	—	—
	U	51	145[1]	—	—	—	—	—	—	—	—
	D	10	0	—	—	—	—	—	—	—	—
II	C	81	147	193[1]	—	—	—	—	—	—	—
	U	69	142	193[1]	—	—	—	—	—	—	—
	D	12	5	0	—	—	—	—	—	—	—
III	C	59	89	112	150[1]	—	—	—	—	—	—
	U	44	78	102	150[1]	—	—	—	—	—	—
	D	15	11	10	0	—	—	—	—	—	—
IV	C	85	115	137	167	185[1]	—	—	—	—	—
	U	71	105	130	167	185[1]	—	—	—	—	—
	D	14	10	7	0	0	—	—	—	—	—
V	C	63	109	132	156	178	202[1]	—	—	—	—
	U	46	95	122	151	175	202[1]	—	—	—	—
	D	17	14	10	5	3	0	—	—	—	—
VI	C	81	120	139	160	190	216	229[1]	—	—	—
	U	65	107	127	151	184	213	229[1]	—	—	—
	D	16	13	12	9	6	3	0	—	—	—
VII	C	70	107	131	145	163	180	200	214[1]	—	—
	U	53	92	120	136	158	175	198	214[1]	—	—
	D	17	15	11	9	5	5	2	0	—	—
VIII	C	85	113	136	156	174	191	203	209	220[1]	—
	U	70	102	127	149	169	189	201	208	220[1]	—
	D	15	11	9	7	5	2	2	1	0	—
IX	C	67	102	127	144	156	184	196	211	227	243[1]
	U	50	87	116	132	149	179	192	210	227	243[1]
	D	17	15	11	11	7	5	4	1	0	0
Per cent Difference		20	10	7	4	3	2	1	—	—	—

[1] Lengths of the age groups at capture.

[2] C = Corrected; U = Uncorrected; D = Difference.

tent of the error depends both on the length at capture of the fish for which the calculations are made and on the year of life for which the calculations are made. The data for males shows virtually the same differences. A striking difference between "corrected" and "uncorrected" calculated lengths exists for age Group I, and is less during the second and third years. Within and between the individual age groups after age II and III these differences tended to decrease progressively with the increase in age. These results show that the use of calculated lengths by direct proportion involves a high degree of error in young fish, producing an underestimate of as much as 20 per cent of the body length of one-year old fish. Lengths calculated by direct proportion, especially for the earlier years of life, may give an erroneous estimate of growth rate based on mean sizes at various ages of white perch. Introducing a correction factor obviates most of this underestimate of growth attainment.

Test of graphical analysis of polymodal frequency distributions:--A new aging technique by a refined Petersen length-frequency method was tested by comparing estimates with age determination based on scale analysis. The method by which arithmetic probability paper may be used in solving bimodal or polymodal frequency distributions has been described by Harding (1949:141–53), and Cassie (1954:513–22). The process theoretically lends greater reliability to counting the modes in the Petersen length-frequency method, which without refinement at best is a crude aging method. The use of probability paper gives a linear transformation of the normal curves which allows the overlapping flanks to be more readily detected, thereby giving a wider range of points which may be used in curve fitting. The application of this graphical method is based on the primary assumption that the polymodal frequency distributions are composed of natural length groups and that the lengths contained within each group are distributed approximately normally about the group mean.

The histogram of observed frequencies of 132 white perch killed by underwater explosives at Point Patience, Patuxent River, Maryland, May, 1948, revealed at least four discernible modes. After plotting the cumulative percentages on probability paper, the first two points of inflection were obvious but subsequent ones were less evident, owing to overlapping of associated groups. Five inflection points, however, indicated the occurrence of five age groups up to the 99% level, beyond which the analysis was terminated due to insignificant numbers. Scale samples (only 115 could be used) showed the occurrence of six age groups (ages II to VII) of which age VII was represented by one fish. There was good agreement between the parameters calculated from the component length groups (A) and the assigned age classes (B). A graphical comparison of significance diagrams of these features showed that A and B of each age group were significantly related. The small size of the sample (especially among ages V and VI) did not produce a normal distribution so that they could not be compared with the same reliability as the first three groups. The probability paper method in this case seems to be a reliable aging technique for the young fish, especially when the ages were verified by scale analysis from the identical sample of white perch. The older age groups were poorly differentiated, hence the method would introduce wide errors among them where the estimates could not be checked by aging based on scale analysis. It was concluded that this method was not an efficient technique for aging white perch populations which included older fish in the Patuxent River.

Source of hydrographic and meteorological data:—Water temperature data were available from the tide-station records maintained and collected at the mouth of the Patuxent River at Solomons, Maryland. There are no continous water temperature records from any other point on the river. Although these temperature records are taken from a region well below the optimum nursery and growing region of the estuary, it is believed, nevertheless, that the temperature record reflects, with a time-lag difference of several degrees, the same temperature conditions upstream. Water temperatures of 15° C. were used arbitrarily to demarcate the length of the white perch growing season, and the number of days between the first record and last record of this temperature was used in the analysis. The early spring growth period in the form of the number of days between the water temperatures from 10° C and 15° C during the spring season was also used in the analysis (Table 9). Field observations have shown that most white perch spawn during April and May when water temperatures range from 10 to 15° C. Salinity data for the 13-year period were available from the records collected by the Chesapeake Biological Laboratory at the mouth of the Patuxent River (Table 9). There are no continuous salinity records from any other point on the river. Since salinity is related to precipitation, a comparison was made with it and the total amount of rainfall in inches for each month over the upper watershed, although it is recognized that local rainfall has very little effect upon salinities in the lower river and bay. In actuality, streamflow from the Susquehanna River, representing Pennsylvania and New York precipitation, is closely correlated with salinity fluctuations in the lower Patuxent estuary (Beaven, 1947:11, and 1960:9).

Mean air temperatures and total amount of rainfall in inches for each month for the 13-year span were obtained from the Monthly Summaries of the Climatological Data of Maryland and Delaware, issued by the U. S. Weather Bureau, in cooperation with the Maryland Weather Service (Table 9). Records from four weather stations in the Patuxent River watershed were compiled: namely, Laurel, Owings Ferry Landing, Huntingtown, and Solomons. Laurel was selected because the records there probably best reflect conditions

TABLE 9. Summary and mean values of various environmental factors originating in the watershed and affecting the Patuxent River and its estuary, based on data recorded at various localities in Maryland and the District of Columbia.

Year	Number of Days Between		Total rainfall (inches) Feb. thru May at Laurel	Mean salinity (‰) Feb. thru May at Solomons	Growing season in number of elapsed days between last and first freeze at 0°C.	Mean temp. °C for May at Solomons		Solar radiation		
								Washington, D. C.		
	Two dates in Spring when H_2O temperature reached 10° and 15° C.	Two dates in Spring & Fall when H_2O temp. first reached and was last recorded above 15°C.						Mean monthly per cent of possible sunshine	Mean monthly heat in gram calories/cm²	
						H_2O	Air	Feb. thru June	Feb. thru June	April
1942	22	192	13.69	15.80	197	19.2	20.5	63.2	406	449
1943	15	167	14.18	10.05	209	17.4	20.1	62.4	413	421
1944	22	179	12.32	14.00	194	19.7	21.5	55.4	370	368
1945	24	212	10.64	12.28	212	16.8	17.8	60.0	413	413
1946	28	204	12.83	11.40	237	18.1	18.8	60.2	393	449
1947	27	186	11.69	13.70	145	17.3	19.0	73.0	435	449
1948	38	188	14.70	12.72	182	17.7	18.8	60.4	384	420
1949	35	198	17.09	10.48	231	18.2	18.7	67.0	391	419
1950	19	190	14.81	12.58	195	16.4	17.3	51.6	377	389
1951	23	188	13.00	9.50	201	17.7	18.5	54.0	407	418
1952	21	190	23.16	9.82	205	17.5	18.2	56.2	412	394
1953	25	194	23.03	10.05	201	20.1	21.1	52.8	388	394
1954	20	198	10.60	13.28	182	17.5	17.6	61.0	443	462
Grand mean	24.5	191.3	14.75	11.97	199	18.0	19.1	59.0	402	418

at the upper estuary. Table 9 also shows the total monthly precipitation in inches between February and May at Laurel, Maryland, on the Patuxent River watershed during the 13-year span. Consultation with Maryland Weather Bureau authorities revealed that available solar radiation records in terms of gram calories per cm² recorded for Washington, D. C. and Baltimore, Maryland, best reflect the amount of sunlight present over the upper Patuxent River watershed. Solar heat energy in terms of gram calories per cm² recorded for Washington was also used. Such records were taken from monthly summaries of Climatological Data—National Summary.

Analysis of data:—Available data, more or less complete, exist for well over 8,000 white perch, largely from the Patuxent River. No attempt was ever made to procure a subjectively "representative" sample, for the possibility of bias being introduced was very great. A non-random sample frequently would result in the selection of fish with certain attributes in disproportionate frequency to the population. Attempts were made to shun the bias of a so-called "representative" sample (Hayne, 1951:133–41); nevertheless, avoiding bias in sampling for white perch in the field was extremely difficult. Wherever possible, scale samples, weights, lengths and other details of individual fish, were taken from all fish tagged or available from commercial fishermen. In cases where a definite size selection, and therefore, sex selection, took place, such as those white perch caught by various gear that were selective for size, a known bias would result and the sample would obviously not reflect the true proportion of sexes in the population. In working with fishermen in a boat in which a large catch was available for sub-sampling, the procedure was to mix all the fish on deck with a shovel as thoroughly as possible, without injuring them for market purposes. They then were shovelled into baskets from different sections of the pile. Where the range in sizes in the same catch tended to be small, but the average sizes of fish of different catches varied considerably, then smaller samples of about 25 to 50 fish were taken, and an endeavor was made to sample more loads.

To reduce the time involved in processing the data, randomized sub-samples, stratified for sex, time, and location, were taken by assigning numbers to scale samples for each fish and selecting them by a table of random numbers. The two equations given by Cochran (1953:54–5) for the determination of the size of sample that must be examined to ensure desired accuracy, when investigating the proportion of a population of a certain sex and age group, aided materially in reducing the work and facilitated the completion of the study. These equations aided in the determination of the size of sample needed from the total available sample of a group of white perch within certain limits of probability. After assigning a margin of error that could be tolerated, set at 5 per cent in this study, appropriate sub-samples were taken from collections of white perch consisting of very large numbers. Cochran's method is the most precise of several methods of estimating the sample size, and it never gave an estimate larger than the original sample.

In most conventional tests, Snedecor (1946) and Dixon and Massey (1951) were used. An attempt has been made, however, to simplify and facilitate the interpretation of large series of frequency determinations by means of graphical analysis of such parameters as the mean, one

standard deviation, two standard errors on either side of the mean, and the range of variation. These collectively are called "significance diagrams," based on methods suggested by Hubbs and Hubbs (1953:49–56, 92), but for reasons cited in the results of subpopulations they were utilized conservatively as suggested by Simpson and Roe (1939:192–4). The significance of the difference between means was interpreted by the suggestions given by Hubbs and Hubbs and Simpson and Roe. Certain aspects of the subpopulation study of white perch based on meristic counts were investigated by the analysis of variance and by a variation of it known as the Duncan multiple-range test, which compares each geographic mean with every other geographic mean (Steel and Torrie, 1960:107–9).

Results

Age, Growth and Year-Class Fluctuations

The objectives of the section are to: (1) review briefly the application of the scale method of aging in the white perch; (2) examine critically the effects of various types of fishing gear on the age and size distribution of the catch; (3) determine the rate of growth for both sexes and to examine fluctuations in growth from year to year; (4) analyze the data for evidence of dominant year-classes; and (5) suggest an index of population density by comparing the first year growth of 13 year classes with commercial catch and hydrographic factors.

Quantitative information on the age structure and growth rate of a population followed from year to year in relation to environment can frequently help in understanding factors that affect dominant year-classes. The growth rate of fish varies far more than does that of a warm-blooded animal. This rate is directly and significantly affected by temperature, and by other physical and biological conditions. Thus, it is possible for different age classes or broods to be roughly the same size, or to have wide differences in average size.

The validity of the annulus as a year-mark in white perch was a primary problem. The scale method is based on the assumption that it is possible to interpret scale pattern correctly to determine the age of fish and to calculate body lengths of fish at previous ages. Van Oosten (1929: 278–9) established several criteria that are widely accepted in fishery studies. He stated that the accuracy of the scale method hinged on three primary conditions. As applied to white perch, they are as follows:

(1) That the scales remain constant in number and retain their identity throughout the life of the white perch: Detailed examination and counts of scales demonstrate that they do not shed or add scales as they increase in age, nor is there a difference in the number of scales formed among variable sizes of very young fish at the time scales are laid down. When the central part of scales from old fish are compared with the scales of young, they are found to be structurally identical.

(2) That the growth of the scale must be proportional to the growth of the body of the fish: Numerous studies have shown that the scale length rarely bears an exact linear relation to body growth in fish. The regression of scale-length on body-length in white perch is proportional, but the intercept is not 0. The lengths at the end of the various years of life calculated from scale measurements agree very well with the corresponding empirical lengths of young age groups whose ages were determined by the examination of scales after the appropriate scale-length/body-length correction adjustment is made.

(3) That the annulus must be formed yearly and at the same approximate time each year: Among white perch there is a definite correlation between age and growth, the number of annuli increasing as the fish grows. The regularity with which there is an increase in the scale length, and hence the number of annuli, is accompanied by increase in the size of the fish, proves that the occurrence of the annuli on the scales is not fortuitous, but that the annuli are added systematically as growth proceeds. Among all the samples taken

during the different seasons for several years, annulus formation was observed only during April, May and June.

Observed age groups and sizes:— Length-frequency distributions and average standard length in millimeters of white perch taken by various gear and methods combined from 1948–1955 are shown by sex and observed age groups in graphic form in Fig. 4. Combination of the data for the several years was possible because, with few exceptions, the corresponding averages generally varied very little from year to year. In the cases where they did vary importantly, the reasons may be assigned to gear selectivity, to smaller sizes and numbers of fish in certain age groups, and to differences in growth rate in different calendar years. In some cases, the trends in discrepancies between lengths observed for fish of different ages were the same in each of the year classes. In spite of the variability of sizes within each group, there generally was a similarity in the size of the fish of the same age and sex taken in different years. The plotting of these lengths against age gives a graphic illustration of the rate of growth. When this observed growth rate is compared with the calculated growth rate, the mean sizes for corresponding ages compare remarkably well (see Fig. 5).

The data in the length-frequency distributions of the observed age groups plotted in Fig. 5 indicates that, in general, the length range of an age group does not vary much according to the age or sex of the fish involved. Among the older fish in both sexes, there is an indication that small numbers affected the range, but generally the standard deviations for all ages except age group I were similar. The generally high degree of overlap of the length-frequency distributions of the successive observed age groups of both sexes, especially among old fish, makes length a relatively poor index of age. This point was evident in the probability-paper method of analyzing polymodal frequency distributions for aging purposes when tested for the white perch. The positions of the modal lengths of age groups I, II and possibly III stand

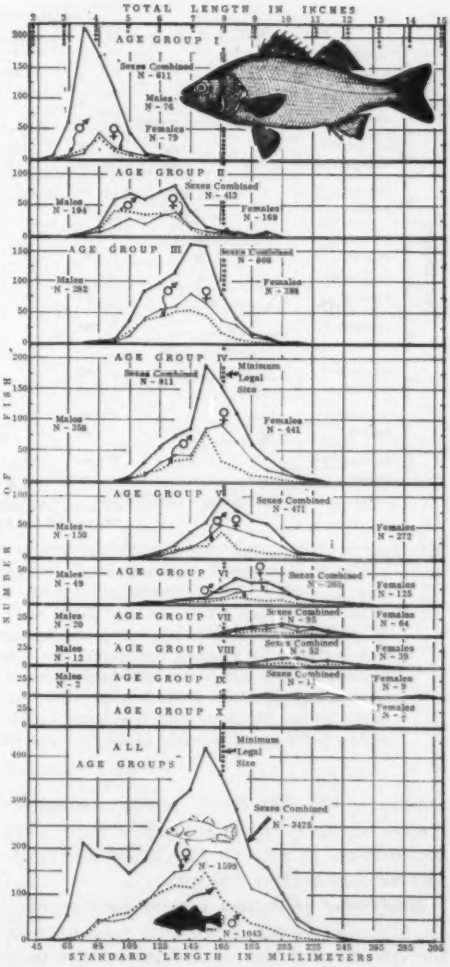

Fig. 4.—Frequency distributions of males, females, and sexes combined, of the white perch, *Roccus americanus*, to show the range of sizes and the magnitude of the unexploited segments by age groups of the population below the minimum legal size of 8 inches T.L.

out distinctly in Fig. 5 for males, females and for all fish combined. Larger white perch at any particular length, however, may belong to any one of several age groups. Among males as many as eight age groups were represented in a single length

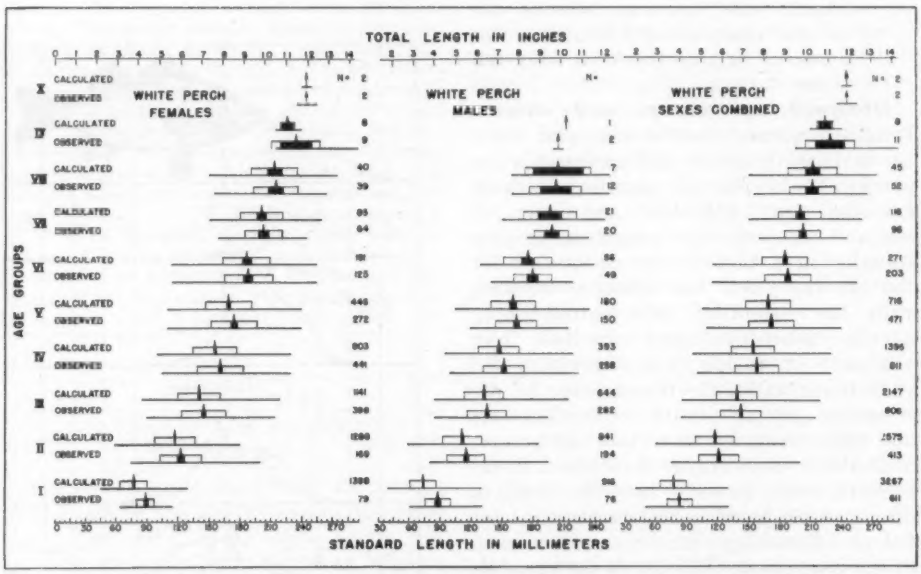

Fig. 5.—Graphical comparison of observed and calculated mean standard lengths of age groups of white perch, *Roccus americanus*. The observed are based on sizes attained by fish at each age group while the calculated are based on sizes computed from back-calculations of intermediate lengths at corresponding ages from scale examination. The range of variation is shown by a heavy horizontal line, the mean by the vertical line. The blackened part of each bar comprises two standard errors of the mean on either side of the mean. One-half of each bar plus the white bar at either end outline one standard deviation on either side of the mean. Reliance can be placed on the significance of the difference between sample means if the corresponding black bars are separated.

interval (150–160 mm), while among females, as many as seven age groups were represented in two length intervals (170–180 mm) and (190–200 mm).

Body-size selection by various gear:— In any discussion of growth rate of fish, the question of the selectivity of the gear used in collecting must be considered. Whether the sample taken is representative of the population as a whole is of great importance in estimating the vital statistics of white perch. Table 10 gives the mean sizes at each age for female white perch taken by various methods of fishing. Data of this type for males also show the same kind of mean differences for various gear. Table 11 gives the mean age of males and females taken by various types of gear. The great differences in these means of relatively large samples indicate that marked gear selectivity occurs. The selective action of commercial gear and other methods of fishing in taking samples depends on the escape of small fish through the meshes. A rough approximation of the maximum size of escape may be obtained by determining the length of fish with a girth equal to the circumference of the largest meshes found in gillnets and haul seines. Since the minimum size of these meshes is set by law (Table 5), at 2½ inches (stretched measure), no white perch with a girth in excess of about 4½ inches should be expected to escape from commercial nets. White perch possess an average girth of this size when they are about 125 mm (almost 5 inches) standard length or about 150 mm (6 inches) total length. Small females with enlarged

TABLE 10. Mean standard lengths in mm of female white perch, *Roccus americanus*, by age groups taken by various methods of fishing in[1] the Patuxent River, Maryland.

Fishing method	Age groups									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Commercial haul seines	—	136.7	155.4	170.9	183.2	199.0	204.6	215.6	232.5	—
N—203		13	40	57	40	23	19	9	2	
Small bag haul seines	89.1	110.0	131.5	150.5	164.8	178.5	—	—	—	—
N—243	78	64	41	42	13	5				
Commercial stake gill	—	—	175.3	187.5	186.3	180.0	215.0	197.5	—	—
N—54			9	14	17	8	2	4		
Commercial anchor gill	—	147.5	157.5	190.8	180.0	179.5	182.5	—	—	—
N—29		1	1	9	6	10	2			
Commercial drift gill	—	—	186.5	181.8	197.5	190.3	201.2	214.3	224.2	237.5
N—29			8	7	8	9	15	17	3	1
Experimental anchor gill	—	128.8	150.2	154.3	179.9	193.6	211.0	224.5	230.0	252.5
N—141		15	34	38	25	14	7	5	2	1
Experimental trap net	—	135.0	154.0	169.4	179.8	195.2	205.5	229.2	292.5	—
N—343		22	67	112	86	37	15	3	1	
Experimental fyke net	82.5	127.5	155.2	156.4	190.0	185.0	—	—	—	—
N—32	1	2	11	14	2	2				
Midstream bownets	—	140.0	144.2	151.0	152.8	—	—	—	—	—
N—83		2	35	26	20					
Dipnets	—	123.7	133.7	143.5	156.4	156.0	185.8	—	—	—
N—322		37	127	97	45	13	3			
Experimental explosions	—	155.8	151.8	168.7	183.8	185.0	197.5	207.5	—	—
N—61		6	22	25	4	2	1	1		
Hook and line	—	128.2	152.5	—	190.5	212.5	—	—	222.5	—
N—17		7	3		5	1			1	
All gear combined	89.0	123.2	145.1	160.7	175.2	188.7	203.4	215.2	234.7	245.0
N—1598[2]	79	169	398	441	272	125	64	39	9	2

[1] The minimum legal length is 170 mm standard length, or 203 mm (8 inches) total length for all types of fishing.
[2] This group contains some females for which the method of capture was unknown.

gonads during spring would be somewhat larger and therefore more susceptible to such gear.

Examination of the length-frequency distributions of the observed age groups for the various gear reveals some interesting facts concerning selectivity. Table 10 shows that mean sizes of females vary greatly for various methods of fishing at corresponding ages. Large-meshed commercial gear took the largest and oldest fish; thus females which were larger at the same age than males would be the more susceptible of the two sexes. Smaller-meshed experimental gear that caught more of the smaller and younger fish apparently did not take many very large and older fish. Gear with very small mesh took very small and medium-sized young fish. These observations are illustrated by the commercial haul seine catch. Age group I is missing, while age group II is poorly represented. The latter group is represented by the larger individuals of young fish, especially among females, that could not escape. Above age group III among both sexes most of the fish were above the minimum susceptible girth-size (123 mm). In sharp contrast, all small and medium-sized fish beginning with age group I above 60 mm were taken by small-mesh experimental haul seines. Table 11 indicates that the youngest of all white perch were taken by this method. Very large and old fish were missing in this gear, indicating that this group of white perch were unavailable or difficult to catch in the shoal habitat where this method of fishing is used.

TABLE 11. Means and ranges of ages of female and male white perch, *Roccus americanus*, taken by all methods of fishing (1948 to 1955), Patuxent River, Maryland.

Method of fishing	Ages in Years					
	Females			Males		
	X	Range	N	X	Range	N
Commercial haul seines	4.61	2–9	203	4.40	2–9	116
Small bag haul seine	2.44	1–6	243	1.98	1–6	197
Commercial stake gillnet	4.85	3–8	54	5.25	3–8	8
Commercial anchor gillnet	5.00	2–7	29	4.29	3–6	17
Commercial drift gillnet	6.24	3–10	68	5.48	3–9	29
Experimental anchor gillnet	4.33	2–10	141	3.41	1–6	64
Experimental trap net	4.32	2–9	343	3.98	2–8	194
Experimental fyke net	3.62	1–6	32	4.07	2–8	14
Midstream bownets	3.77	2–5	83	3.57	2–5	35
Bank dip net	3.62	2–7	322	3.40	1–6	279
Experimental explosions	3.69	2–8	61	3.47	2–7	49
Hook and line	3.71	2–9	17	4.25	1–7	40
All gear combined	3.97	1–10	1598	3.49	1–9	1043

The same generalizations indicated above apply to commercial gillnets. The largest and oldest fish on the average were taken by commercial drift nets. Commercial stake gillnets and anchor gillnets also caught large and old fish. When the mesh size of gillnets was somewhat reduced as in experimental anchor gillnets, the smaller old and larger young fish were taken. The females were somewhat older than the over-all average. Experimental, small pound-like trap nets caught large fish that were older than the over-all mean age of fish for all gear combined. The largest fish taken in the Patuxent River during this study, a female with a total length of over 13 inches, and from age group IX, was taken in this gear. Fish taken in experimental fyke nets were close to the average size of most fish. For almost all other gear, the females, on the average, were larger and older than the males taken in the same gear. For some reason, however, the mean age of the males in fyke nets was higher than that of the females. The only other cases where this was true occurred among males taken by commercial stake gillnets, and fish caught by hook and line. Bank dipnets and midstream bownets were operated in close proximity to one another in tidal freshwater, but the latter caught somewhat larger and older fish owing to the larger mesh size in this gear. Experimental explosions and hook and line apparently sampled average-sized and close to mean-aged fish in the same general habitat of relatively deep water. The mean ages for fish taken by all methods of fishing were: females—almost 4 years old; males—3½ years old.

TABLE 12. Observed weights of 484 male and 807 female white perch, *Roccus americanus*, Patuxent River, Maryland.[2]

Age	Females				Males				Diff. in means
	Number of fish	Mean in grams	Stand. dev.	Stand. error of means × 2[1]	Number of fish	Mean in grams	Stand. dev.	Stand. error of means × 2[1]	
I	85	21.7	9.44	2.04	73	18.8	7.75	1.82	2.9
II	97	53.0	36.62	7.44	114	42.9	30.50	5.72	10.1
III	165	106.4	59.06	9.20	113	73.1	37.59	7.08	33.3
IV	186	125.3	57.40	8.42	98	108.2	44.99	9.08	17.1
V	134	157.8	71.97	12.44	57	140.8	58.86	15.60	17.0
VI	71	193.9	83.64	19.84	21	158.3	64.68	14.12	35.6
VII	32	240.3	85.27	30.12	8	188.8	99.42	70.02	51.5
VIII	28	322.1	123.21	46.58	—	—	—	—	—
IX	7	449.3	186.9	141.06	—	—	—	—	—
X	2	470.0	—	—	—	—	—	—	—

[1] Twice the standard error on either side of the mean for both sexes is given for ready comparison of means at each age.

Observed weights and length-weight relationships: — The average observed weights of the age groups of white perch shown in Table 12 demonstrated that females were heavier at each age than males. Considerable variation, however, is shown by the standard deviations on either side of the mean at different ages for the two sexes. It is greatest among the older, sparsely-sampled groups, and least among the younger, sexually-immature fish. The data indicated that there is a definite seasonal variation in the weights. During winter and spring prior to spawning, both sexes, especially the females, are heavier than at any other season due to the maturation of the gonads. They are lightest in weight during early summer after spawning when their gonads are resting and undeveloped.

[2] It is pertinent to note that most white perch throughout their geographic range do not greatly exceed average lengths and weights given in this paper. Norris (1865:91), who was considered a reliable early observer on the biology of fishes by Goode and Gill (1903:36), stated that "Its average length is eight or nine inches; it is not often more than twelve, though in rare instances it is found fourteen inches long." Goode and Gill (1903:37–8) and many other early writers suggested that both netters and anglers consistently harvested comparatively small fish, a fact that disputes the recent claim from some quarters that overfishing and improper management have reduced the average size of this species throughout its range. Underexploitation and overcrowding of the white perch, of course, have contributed toward this result. Large specimens over 12 inches and 1½ pounds are scarce. Radcliffe and Welsh (1917:42) recorded an individual 350 mm (13.7 inches long) weighing 1¼ lbs, remarking that individuals 260 and 280 mm (10 to 11 inches long) weighing one pound were abundant. They also stated, however, "Small individuals, however, are so exceedingly numerous that the average weight per fish, as taken in pound-nets, runs from .15 to .17 lbs." The maximum size of white perch recorded by Hildebrand and Schroeder (1928:452) was 11 inches; their samples ranged from 55 to 280 mm. The largest white perch encountered during the present study came from a freshwater pond at Sands Point, Bohemia River drainage in the upper Chesapeake Bay area, Cecil County, when the impoundment was rotenoned and drained on October 15–16 1956. The two females were as follows: smallest, 13.4 inches T.L., weight, 1 lb, 8 oz, and the largest, 14.3" T.L., weight, 1 lb, 9 oz, in age group VII. Elser (1956:1, 4) pointed out that the 10-acre pond contained 4,000 pounds of fish, of which 11 pounds were white perch, ranging from 4.4 to 14.3 inches, including the two aforementioned specimens. Raney and McClane (1951:1301–2) remarked that "The average size is about ½ pound but under the best food conditions the maximum size is thought to be about 6 pounds. The present world's record, caught by rod and reel, is 4 pounds, 12 ounces [= 19 inches (Thoits, 1958:4)], caught in 1949 in Belgrade Lakes, Maine. It commonly reaches a length of 9 to 10 inches."

The observed weights of females exceeded those of males on the average by almost 24 grams. The advantage of the females increased to over 33 grams in the third year, then decreased until the sixth and seventh years when there was a difference of over 35 and 51 grams, respectively, between males and females.

An important aspect of growth is the relationship between length and weight. Stroud (1955:23) is one of the few workers who has published a graph of the relationship in the white perch. It is frequently necessary to estimate the weights of fish from their lengths. For this reason, data have been compiled on the length-weight relationship of the white perch, and a mathematical relationship for both sexes was calculated. Since length is only one of many possible linear measurements, and since growth is generally allometric, the relationship between length and weight remains close to the cube among fishes. This fact implies that changes in form with age are relatively conservative. The length-weight relationship was calculated for 888 females and 580 males. By converting the natural numbers to logarithms, the exponential relationship can be conveniently expressed as the linear equation,

$$\text{Log } W = k + n \text{ Log } L,$$

where: W = weight in grams
k = constant
n = relative growth constant
L = length

The equations of the fitted lines for both sexes are given in Fig. 6, which for practical purposes are not considered different. They denote a constant percentage relationship between length and weight. Thus, a constant relationship between the multiplication of weight and the addition of length is expressed by the data.

Calculated lengths of the age groups: —The use of scale measurements in back-calculating body lengths is an important procedure by which past sizes may be determined after certain growth relationships are assumed between scale and body lengths of white perch. Fig. 5 shows graphically the relationship between calculated and observed lengths at each age for males, females and all fish combined. Tables 13 and 14 summarize the data used in charting the growth histories. Corrected mean calculated lengths for the different age groups for both sexes and the data combined show very good agreement with the mean observed lengths for corresponding age groups. Significance diagrams show some statistical differences from age groups I to IV in females, and I to V in the sexes combined. In all cases, the mean calculated length is lower than the observed size at each age. These differences are real, and are believed to be largely brought about by gear selectivity and by growth added during the year of capture of fish in the observed age groups. Thus, the latter group would be expected to be somewhat larger, especially among younger fish where growth is greatest. Tables 13 and 14 also show that calculated growths based on different age groups in the same year's collection or upon

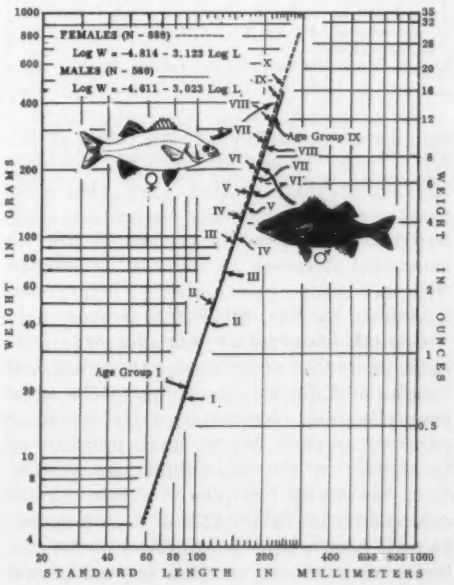
FEMALES (N = 888)
Log W = -4.814 - 3.123 Log L
MALES (N = 580)
Log W = -4.611 - 3.023 Log L
Age Group IX
Age Group I
WEIGHT IN GRAMS
WEIGHT IN OUNCES
STANDARD LENGTH IN MILLIMETERS

Fig. 6.—Length, weight, and age relationship of white perch, *Roccus americanus*, with the age groups of the two sexes located on the line according to average length and weight from Patuxent River samples. Note use of log scale.

TABLE 13. Calculated growth at the end of each year of life of the females of each year class of Patuxent River white perch *Roccus americanus*.

Year class	Number of fish	Calculated length at end of year of life (Females)									
		1	2	3	4	5	6	7	8	9	10
1942	2	82	105	128	145	168	180	—	—	—	—
1943	10	71	107	138	160	178	195	202	208	242	255
1944	29	76	114	145	163	188	205	217	230	232	248
1945	40	78	118	142	153	171	186	194	208	224	—
1946	94	82	123	147	165	180	191	203	217	—	—
1947	100	81	122	144	161	170	184	198	—	—	—
1948	203	80	121	142	157	168	179	—	—	—	—
1949	266	78	119	140	152	168	195	—	—	—	—
1950	290	78	116	138	153	162	—	—	—	—	—
1951	171	78	117	141	154	—	—	—	—	—	—
1952	83	71	106	132	—	—	—	—	—	—	—
1953	56	63	97	—	—	—	—	—	—	—	—
1954	42	71	—	—	—	—	—	—	—	—	—
Grand averages and total	1386	77	118	141	156	169	187	202	214	226	245
Average increments of growth		77	41	23	15	13	18	15	12	12	19
Maximum differences		19	26	19	20	26	26	23	22	31	—
Equivalent total length in mm.		95	145	173	192	208	230	248	263	278	301
Equivalent total length in inches		3.7	5.7	6.8	7.6	8.2	9.1	9.8	10.4	10.9	11.8
Number of fish		1386	1288	1141	803	446	191	85	40	8	2

TABLE 14. Calculated growth at end of each year of life of the males of each year class of Patuxent River white perch, *Roccus americanus*.

Year class	Number of fish	Calculated length at end of year of life (Males)								
		1	2	3	4	5	6	7	8	9
1942	1	98	128	142	162	172	188	—	—	—
1943	7	71	108	128	144	164	142	152	162	—
1944	12	77	126	145	161	220	228	240	252	—
1945	28	74	118	143	161	173	186	198	202	212
1946	39	81	124	144	160	174	180	194	204	—
1947	53	81	118	142	156	167	176	210	—	—
1948	131	76	116	135	147	153	178	—	—	—
1949	155	76	115	132	141	155	132	—	—	—
1950	183	76	114	130	146	175	—	—	—	—
1951	117	72	111	125	146	—	—	—	—	—
1952	94	66	96	117	—	—	—	—	—	—
1953	57	62	91	—	—	—	—	—	—	—
1954	38	70	—	—	—	—	—	—	—	—
Grand averages and total	915	74	112	133	148	161	175	197	205	212
Average increments of growth		74	38	21	15	13	14	22	8	7
Maximum differences		36	37	28	21	22	12	10	2	—
Equivalent total length in mm.		910	138	164	182	198	215	242	252	260
Equivalent total length in inches		3.6	5.4	6.5	7.2	7.8	8.5	9.5	9.9	10.2
Number of fish		915	841	644	393	180	56	21	7	1

samples of the same year class taken at different ages, agrees satisfactorily for corresponding years of life. They also show that when different year classes are compared at corresponding periods of life, no consistent decrease in calculating lengths with increasing age (i.e., Lee's Phenomenon as defined by Hile, 1936:222) is observed.

Growth histories of year classes:—Disagreements that occur among the calculated lengths of different age groups of the same year class can be attributed for the most part to variation due to small numbers of specimens in the individual age groups. Gear selectivity has played a role, but as can be seen in Tables 13 and 14, the agreement is good where the numbers of fish are large, as is shown between the calculated lengths of the first year of the 1949–1951 year classes for females, and the 1948–1950 year classes for males.

A graphical representation (Figs. 7 and 8), based on the data in Tables 13 and 14, shows the extent to which the growth histories of the year classes may differ. Differences in growth exhibit a wide range of variation among the year classes in the relationship of length to age, particularly in the earlier years of life. In both sexes the differences between the largest and smallest calculated lengths of year classes at corresponding ages were of the same general magnitude from the first to the ninth year of life. Data for later years of life for both males and females were irregular. Differences in the growth of year classes may lead also to variations in different calendar years in the relationship of length to age. The light lines of Figs. 7 and 8 that connect the calculated lengths for corresponding years of life, show that both sexes of white perch were smaller at age I and II in 1953 than in the preceding calendar years. In other years especially in 1946 and 1947, the Patuxent River white perch were relatively large for their age.

Figs. 7 and 8 also show that, on the average, differences in growth between the

growth at corresponding ages for each sex during these periods is good. The irregularities in the general trend of the data on the fluctuations in the relationship of size to age in different calendar years are also not very great. It is evident, for example, that the 1944 and 1946 year-class among females exhibited a more rapid growth rate than 1945 and 1947 hatches. Irregularities are most perceptible among the oldest age groups, where some errors in age determinations may have occurred. The rejection of all highly questionable scales, however, has minimized the possible effects of errors from this cause. It is believed, therefore, that observed differences in growth between year classes are real.

The calculated lengths of all collections for both sexes have been summarized to show relatively smooth curves of growth in length for the Patuxent River white perch (Figs. 9 and 10). It must be recognized, however, that the curves are only roughly descriptive of the true typical growth. Some idea of the variation among calculated estimates at different ages can be seen graphically in Fig. 5. The fact that annual fluctuations in growth rate occur, as shown in the growth histories of the year classes, indicates that a clearly defined general growth curve probably does not exist in nature. The calculated growth curves for the sexes have the same general form. The females grow at a distinctly higher rate and live longer than males, maintaining a larger size at all ages. The growth of each sex in the first year was greater than in any other year of life. The average increments of growtn shown in Tables 13 and 14 were of the same magnitude in the two sexes, decreasing rapidly after age II. The females, however, seemed to have relatively higher increments at the more advanced ages than did the males.

Abundance of age groups and year classes:—A tabulation of the age, sex and year-class composition of each year's collection of the Patuxent River white perch for the period 1948–1955, by all methods of collection combined, appears in Table 15. In this an attempt was made, assuming that the samples were adequate, to perceive a high number of old age group indicative of a strong year class, and a scarcity of fish in a young age group showing a poor year class. The very young fish must be disregarded in such an analysis since they are inadequately represented due to gear selection. In general, the representation of the two sexes in the age groups and year classes was similar, hence the combination of the data. If age groups I and II are disregarded in Tables 15, there does not appear to be a decidedly unequal representation of the different age groups. Collections made from 1952 to 1955 contained a disproportionate number of fish taken by small bag haul seines that were used to

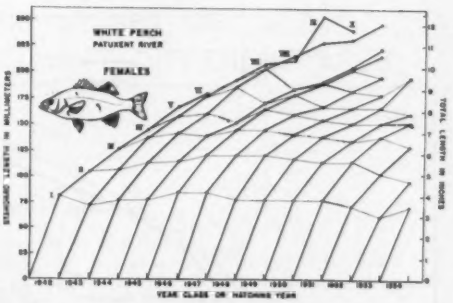

Fig. 7.—Calculated growth histories of year classes of female white perch, *Roccus americanus*, from the Patuxent River, Maryland. The calculated lengths of corresponding years of life in different calender years have been connected with dark lines.

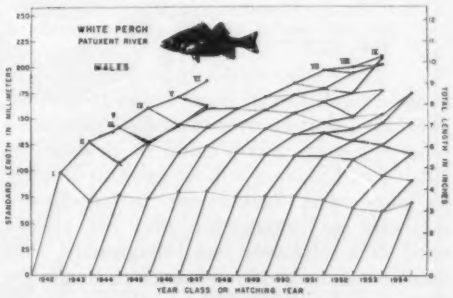

Fig. 8.—Calculated growth histories of year classes of male white perch, *Roccus americanus*, from the Patuxent River, Maryland. The calculated lengths for corresponding years of life in different calendar years have been connected by dark lines.

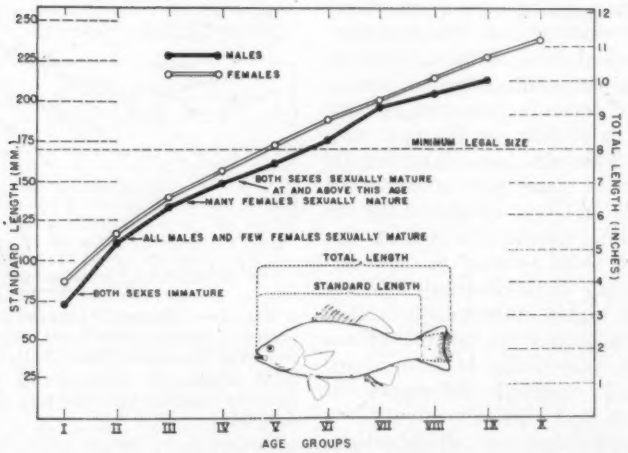

Fig. 9.—Grand average calculated lengths and calculated increments of growth in length for each year of life of female and male white perch, *Roccus americanus*, Patuxent Rixer, Maryland.

sample small fish in shoal areas. It may be concluded that no overwhelming dominance of a single age group could be detected in this data. Evidence will be presented below to show that fluctuations in population densities may occur, but they are apparently of a relatively small magnitude. Any attempt to detect the presence of relatively strong or weak year-classes based on an examination of percentage occurrence of various ages is fraught with many difficulties. There is a great danger that some data may not provide an exact measure of the true relative strength of the year classes unless rigid criteria for the collection of the sample is employed. The most important difficulty in the interpretation of the material is related to the effect of age which the year classes appeared in the collections, region of collections, and to gear selectivity. It is tentatively concluded that spectacularly dominant year classes are not indicated in the Patuxent River data.

Relationship of Meteorological, Hydrographic and Population Density Factors on First-Year Growth of White Perch, 1943–1954

The purpose of this section is to study the relationship, using correlation analysis, between certain environmental variables and population density and the first-year growth of 13 year classes of white perch. No attempt will be made to demonstrate a cause and effect relationship, rather, where the data indicates that possible association between two variables exists at a certain statistical confidence level, it will be cited as such. The first-year growth rates were selected for the following reasons:

(1) the greatest increments in length occur during the first year of life, and it is believed that these increments would best indicate any changes in the annual growing conditions. The multiple effects of several years of growth are also avoided;
(2) increments are independent of growth incurred in other years; and
(3) although a statistically significant difference occurs in the means of the standard lengths of the two sexes in the first year growth, these were small enough so that both sexes, with fish of unknown sex, were combined. The first year growth rates were generally similar in the various regions of the Patuxent River. Genetic differences could not be discerned.

The selection of the meteorological and

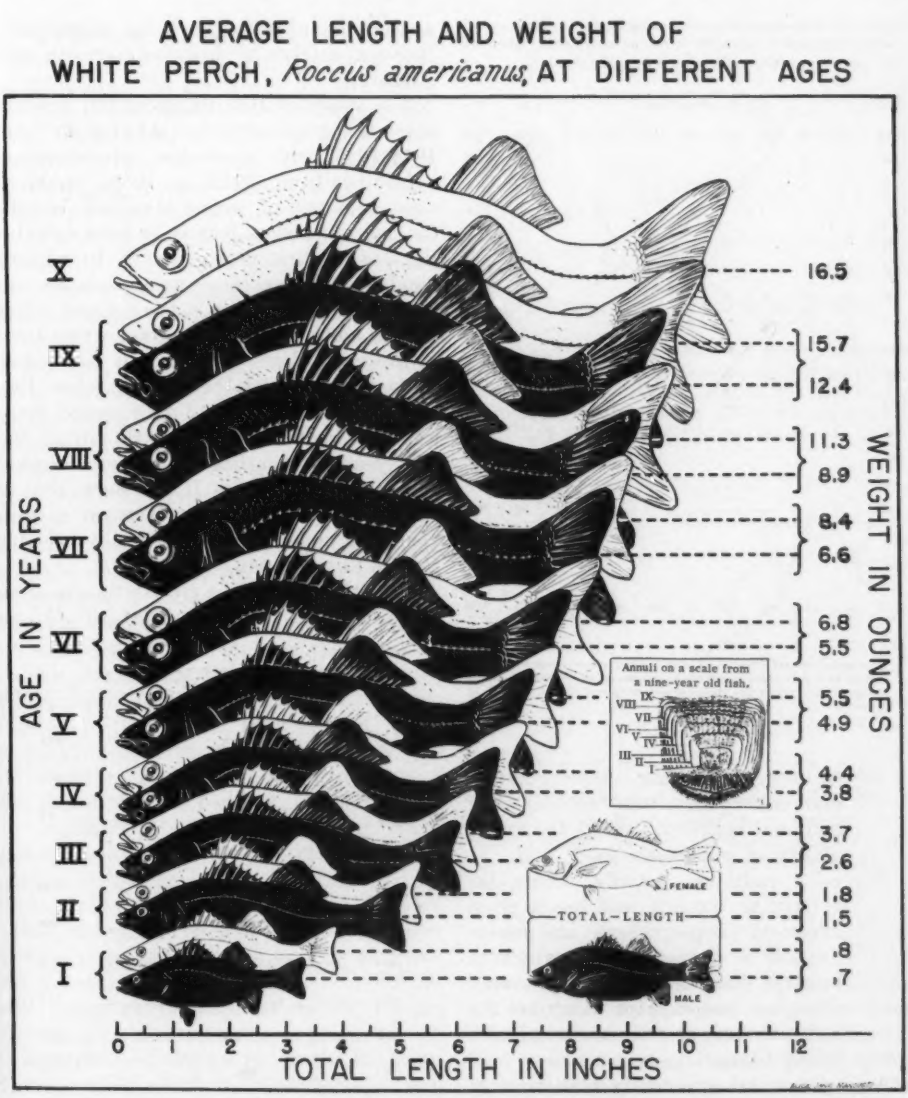

Fig. 10.—Graphic summary of average calculated length and weight of white perch, *Roccus americanus*, at different ages, based on Patuxent River samples.

hydrographic factors was limited to available and authoritative long-range data (see Table 9). They were studied for the following general reasons:

(1) water temperature affects growth rate and metabolic activity. First-year growth was associated with periods between certain water temperature levels;

(2) rainfall has a great effect on variation in water volume, flow and temperatures on the spawning and nursery grounds, and affects growth indirectly;

TABLE 15. Year class composition of each year's collection of all sexes combined of white perch, *Roccus americanus*, taken by all methods of fishing, Patuxent River, Maryland.[1]

YEAR	YEAR OF COLLECTION								AGE	
Class	1948	1949	1950	1951	1952	1953	1954	1955	Group	Total
1940	2	3	-	-	-	-	-	-	-	5
1941	5	7	1	-	-	-	-	-	-	13
1942	11	14	4	-	-	-	-	-	-	29
1943	25	23	10	9	1	1	-	-	-	69
1944	67	33	17	6	3	-	1	-	-	127
1945	74	60	30	16	8	4	6	-	-	198
1946	23	34	57	40	26	28	23	-	X	231
1947	-	15	71	47	35	64	23	-	IX	255
1948	-	1	22	39	72	216	41	1	VIII	392
1949	-	-	1	13	47	338	80	5	VII	484
1950	-	-	-	2	18	359	137	12	VI	528
1951	-	-	-	-	107	150	144	33	V	434
1952	-	-	-	-	-	260	94	38	IV	392
1953	-	-	-	-	-	-	146	78	III	224
1954	-	-	-	-	-	-	-	94	II	94
1955	-	-	-	-	-	-	-	-	I	-
Total	207	190	213	172	317	1420	695	261	-	3475

1/ The diagonal lines and arrows to the left of the Roman numeral age designations indicate the number of fish in each age group taken during the year of collection. The age of each group is also derived by subtracting year class from year of collection.

(3) salinity affects the osmoregulation and other metabolic activities of fish, and indirectly affects the availability of planktonic food; and

(4) solar radiation usually occurs inversely to rainfall, and has a great effect on photosynthesis and reproduction in phytoplankton, which in turn, as food, can have a profound effect on zooplankton, and on the survival and growth of larval and young fishes.

An indirect but apparently real index of population density of white perch in the Patuxent is the commercial harvest by a relatively stable and known number of fishermen and gear for the period from 1944 to the present. Careful examination of the effort expended each year by haul seines indicated that it was also similar from year to year. The most complete data exists for commercial haul seines, and since their catches are related to the abundance and availability of white perch, the relationship between catch and first-year growth was studied.

The study of 3155 Patuxent River white perch taken during the period of study from 1948–1955, with year-class representation extending from 1942 to 1954, produced measurements of mean standard lengths for each year based largely on back calculations of the first year's growth. In a small number of cases these measurements are based on 0-year old fish captured after growth had ceased due to lower water temperatures in late October and November of the year in which they were hatched. Fig. 11 shows that for the 13-year period there were different rates of growth during the first year for yearling white perch during various calendar years. It also shows that in certain cases the means between certain years are apparently significantly different for the 13-year span.

Growth span:—The growth time in days between water temperature at 10° C and

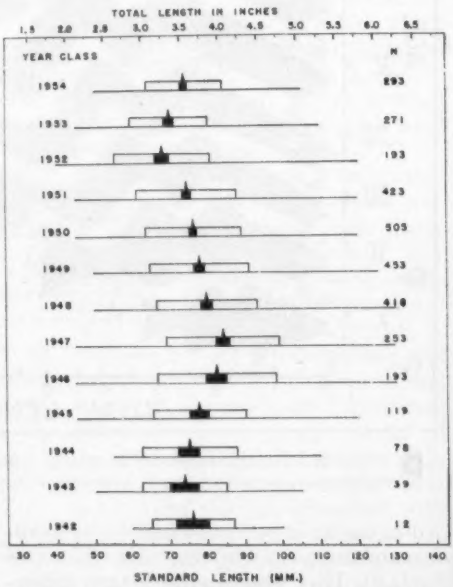

Fig. 11.—Mean calculated standard lengths and various parameters for first-year growth of white perch, *Roccus americanus*, arranged by year-class from 1942–1954, Patuxent River, Maryland. See legend of Fig. 5 for interpretation.

15° C (Table 9) was related to the first-year growth of white perch in the various calendar years. The coefficient of correlation calculated for these variables was 0.483. The significance of this coefficient was tested by Fisher's "t" test. The probability of obtaining a value numerically greater than this value, 0.483, if no correlation existed between the two sets of variates, was calculated to be 10 per cent. Fig. 12 shows the direct relationship between growth and time in days between 10° C and 15° C. It seems likely that a relationship exists between the variates. This association suggests that a longer period of ascending spring water temperature may stimulate a greater growth rate.

The association between the first-year growth of white perch and the elapsed time in days between the first and last temperature of 15° C (see Table 9) just below the water's surface in spring and fall was also determined. A value of 0.315 was obtained by this coefficient, and this value would be exceeded 30 per cent of the time by chance alone. Thus, the first-year growth of white perch does not appear to be closely related to the elapsed time between these water temperatures. An examination of the data of the elapsed time between 10° and 15° C and for the period between 15° and 15° C as well as a graphic comparison, indicated that they were not closely associated, and that each period of time had its own effect on white perch growth. Hassler (1956:114) also has shown that for sauger first-year growth, the two periods of growing seasons (one, between 50° to 60° F, and the other, between 60° to 60° F) did not appear to be related.

Rainfall:—Precipitation in the Patuxent River watershed varies considerably from year to year. The degree of association between the combined mean monthly rainfall from February to May at Laurel in the mid-upper Patuxent River watershed (Table 9) and first-year growth of this species was determined. The coefficient of correlation between the first-year growth of white perch and combined precipitation for the four month period was -0.597, $p = <0.01$. Hassler (1956:115) also found this

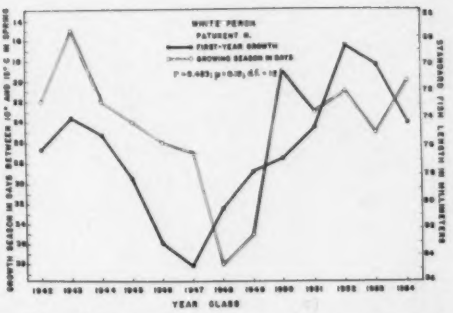

Fig. 12.—Relationship between first-year growth of white perch, *Roccus americanus*, and number of days in early spring between the first water temperature at 10° and at 15° C for the 13-year span, 1942–1954, Patuxent River, Maryland.

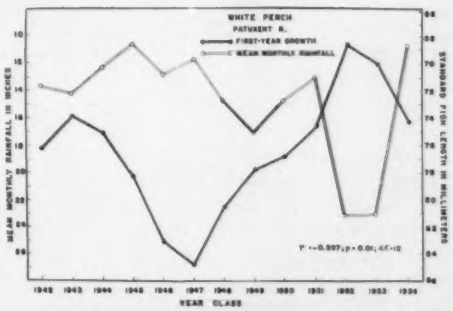

Fig. 13.—Relationship between first-year growth of white perch, *Roccus americanus*, and the combined February to May rainfall in inches for the 13-year span, 1942–1954, Patuxent River, Maryland.

relationship to be negatively correlated at about the same level for the sauger in Tennessee. A graph illustrating the association of February–May rainfall and first-year white perch growth is presented in Fig. 13. The association suggests that heavy spring rains would be related to a depression in the first-year growth. Heavy rainfall could bring this about by affecting the spawning and nursery areas. Increased turbidity, fluctuating temperatures and variable waterflow would affect both food availability and the distribution of young fish. Since heavy rainfall spread over a long period of time is associated with low solar radiation, the combined effects of both would be expected to lower plankton production.

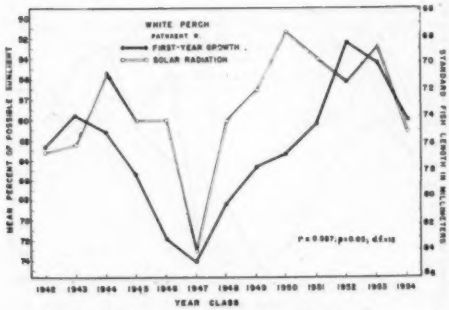

Fig. 14.—Relationship between first-year growth of white perch, *Roccus americanus*, in the Patuxent River, Maryland, and mean monthly per cent of possible sunlight from February to June at Washington, D. C., for the 13-year span, 1942–1954.

Salinity:—The coefficient of correlation between the first-year growth and salinity at Solomons, Maryland, from February to May for the 13-year period (Table 9) was calculated. The coefficient was 0.399, and a *t*-test indicated that to find a value greater than this could occur by chance, if the variables had no correlation, less than 20 per cent of the time. Thus, the two sets of variates did not appear to be closely related. An explanation is found in the correlation of salinity and rainfall. The correlation coefficient between the total precipitation from February to May at Laurel, Maryland, and average monthly salinity for the same four month period at Solomons, Maryland, for the 13 years was −0.542, a negative correlation significant at the five per cent level. Thus, high salinities are related to low precipitation. As stated before the Patuxent River stream flow does not have as large an effect as the Susquehanna River on salinity at the mouth of the estuary and the bay at Solomons. Beaven (1947:1–11) stated that stream flow from the Susquehanna River represents over 85 per cent of all contributions north of the Potomac River and over 95 per cent of that above the Patapsco. The explanation of the relatively significant negative correlation between rainfall at Laurel, with its subsequent freshwater runoff, and salinity at Solomons, probably lies in the fact that precipitation and subsequent stream flow in both the Susquehanna and Patuxent Rivers occurred generally at the same time and perhaps with the same magnitude.

Solar radiation:—Two types of solar radiation were compared with first-year growth of white perch. One, the average monthly per cent of possible sunshine for the five month period, February–June, 1942–1954, recorded at Baltimore, Maryland, and Washington, D.C. (see Table 9), both near the Patuxent River spawning and nursery area, represented a measurement of light energy available for photosynthetic action among phytoplankton. The other, gram calories per cm^2 of solar radiation for the same period of time recorded at Washington, represented a measurement of heat energy, although both are obviously interrelated. It is interesting, therefore, that the coefficient of correlation between first-year growth and light energy for Washington ($r = 0.597$; $p = <0.05$) and Baltimore ($r = 0.496$; $p = <0.10$) showed that the two variables were related (see Fig. 14). Solar data in terms of gram calories for each month from February to June was correlated with first-year growth, but no correlation was indicated between the two variables except for April ($r = 0.532$; $p = 0.05$). The variability of the heat energy data is such that the statistically significant value for April could have arisen by chance, hence it is unacceptable. The results suggest that if the associations between light and growth are real, then the former possibly exerts some effect indirectly on food production for young white perch. It is plausible that a high amount of light energy spread over the spring season accelerates photosynthesis of chlorophyll-bearing aquatic plants. This action might result in a high production of phytoplankton which in turn indirectly might bring about faster growth of young fish. Thus, the direct correlation suggests that a small amount of the average monthly sunlight in spring brings about the smallest average sizes of first-year growth, and the opposite effect at high values. The relationship between heat energy and first-year growth for the same period and location indicates that the former may be so

variable over the spring season that its effects are not as significant as light.

Agricultural growing season:—The data for the elapsed time in days of the agricultural growing season (see Table 9) was compared with the first-year growth of white perch. The agricultural growing season as represented by the time between the dates of the last freezing temperature in spring and the first freezing temperature in fall, was found to be unrelated to the first-year growth of white perch. The agricultural growing season is sometimes used as an indicator of growing conditions in lakes and other bodies of water, and the growth of fish in such an environment is reflected by changes in the environment. The lack of any apparent relationship between growth time between frosts and first-year growth of white perch indicates, as was pointed out by Hassler (1956:113) for the sauger in Tennessee, that the practice of evaluating previous environmental conditions in various waters and the duration of fish growing seasons by the use of "time between frosts" is of little value.

Air temperatures at Solomons were compiled and analyzed for the months of April and May for the 13-year period (May values in Table 9), in order to determine if any association existed between these temperatures and water temperatures. These were highly correlated, 0.937 for April and 0.874 for May, both far above the 99 per cent confidence limit. Since the elapsed time in days between 10° and 15° C in water temperatures occurred largely during April, and since this time was significantly correlated with first-year growth at the 95 per cent confidence level, it is probable that some relationship occurs between April air temperatures and first-year growth of white perch. A detailed and accurate knowledge of this relationship is valuable for predicting air temperature effects upon first-year growth of white perch in the absence of water temperature data for a long period of time.

Index of population density:—The indirect index of population density in the form of the commercial haul seine catch for the span of 1947–1955 (see Table 1) was

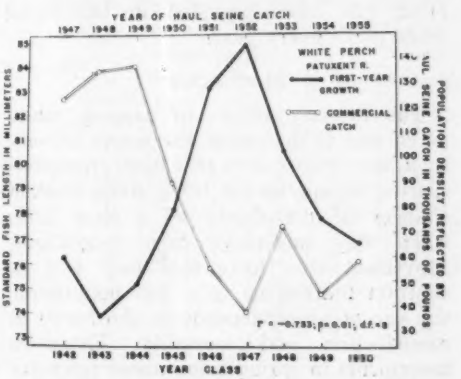
YEAR OF HAUL SEINE CATCH
1947 1948 1949 1950 1951 1952 1953 1954 1955
WHITE PERCH
PATUXENT R.
FIRST-YEAR GROWTH
COMMERCIAL CATCH
STANDARD FISH LENGTH IN MILLIMETERS
POPULATION DENSITY REFLECTED BY HAUL SEINE CATCH IN THOUSANDS OF POUNDS
r = −0.753; p=0.01; d.f.=8
1942 1943 1944 1945 1946 1947 1948 1949 1950
YEAR CLASS

Fig. 15.—Relationship between first-year growth of white perch, *Roccus americanus*, from 1942 to 1950 and index of population density in terms of the commercial haul seine catch in pounds from 1947 to 1955, five years later when the fish enter the commercial fishery, for a nine-year span, Patuxent River, Maryland.

correlated with first-year growth that occurred in the fish 5 years earlier for the span 1942–1950. This approach is based on the fact that the bulk of a year class does not reach legal size and enter the commercial fishery until it attains age group V (Fig. 9). A negative correlation coefficient which was −0.753, highly significant at the 99 per cent confidence level at 8 degrees of freedom, was calculated. This value suggests that size of white perch is inversely related to population density. Fig. 15 shows this remarkable relationship. A departure from the highly significant relationship occurs during the last 2 years that are compared. No explanation is available, except that the lower catch may be associated with economic factors. Generally, the commercial haul seine catch is considered a reliable index to population abundance of white perch. Table 1 gives the commercial production of white perch by various gear in the Patuxent River for the period 1944–1955. In 1941, the Maryland Fish Management Plan stabilized by law the number of fishermen and gear in tidal waters, so that the effect upon the Patuxent River fishery has been to maintain a relatively stable fishery. A canvass of the haul seine fishery indicates that generally the same

effort has been expended in harvesting white perch every year.

Movements

The primary object of tagging white perch was to determine the extent of seasonal movements. As a schooling, gregarious species, the species can bring about marked changes in availability on a local basis when they undertake their migrations. Movement is a force that may add or subtract individuals in a fish population, the size of which depends on the forces of reproduction and mortality. Extensive movements in spring bring about intensive fishing and some natural mortality to adult fish. Reproduction, which is the primary stimulus for migration, produces great additions to the population. At first, as in all animal populations, recruits are greater than deaths, but at capacity in a relatively constant environment, recruits will equal deaths. Thus, the net effect of immigration and emigration is of primary importance to population numbers of white perch in this study. In the beginning of the study, it was not known whether the white perch in the Patuxent River consisted of local populations in the estuary, whether they left the River, or whether they migrated to Chesapeake Bay to spawn or overwinter. Accordingly, an attempt was made to determine:

(1) the pattern of white perch migrations in spring during the spawning period;
(2) the nature of movements during the summer months when they are feeding and growing;
(3) their distribution in the estuary during fall and winter months; and
(4) the relative homogeneity of the Patuxent estuary population.

In addition, the mean distance traveled in miles, freedom interval in days, and rate of speed during the various seasons was calculated.

During the four-year tagging study 324 white perch, or 10.7 per cent of all tagged fish, were recaptured with sufficient information available to calculate the distance they had migrated from the point of release. Table 17 gives details of the recoveries by zones in the Patuxent River and outside the estuary mouth. Only three recoveries, representing less than two per cent of all recaptured fish were found outside the Patuxent River estuary. In general, the tagged fish were subjected to a relatively intensive and variable fishery (Table 5). Haul seines, operated largely in the mid-estuary accounted for over one quarter of the recoveries, while gillnets of all types, generally distributed between zones II and V, took slightly less than one quarter of the fish. Anglers took less than eight per cent of all the tag returns. Tags from recaptured fish were returned by fishermen during every month of the year, indicating the generally sustained nature of the fishery. Fishermen operate nets or angle in much of the Patuxent River estuary during most of the year so that it is reasonable to believe that the returns represent the movements of fish rather than fortuitous fishing.

The dispersion of tagged fish shows that white perch make relatively extensive movements in the Patuxent River estuary. Table 18 summarizes the distances traveled in miles from the zones of tagging, either upstream or downstream, by white perch as indicated by tag recoveries. From Zone I made up of tidal fresh water the bulk of the fish dispersed downstream. Those that moved upstream in this region traveled no more than a few miles. The fish tagged in Zone V in high brackish water (Table 2) generally moved upstream. There is a seasonal variation in movement: during spring, as indicated above, movements are extensive. During summer and fall, they are curtailed (Table 20). Table 18 shows that 46.3 per cent of the recoveries for all seasons were within a few miles of the point of tagging. The next large group of recoveries, 16.4 per cent, were made between 25 and 30 miles from the tagging sites. All other intervals of miles were represented by less than 10 per cent of the recoveries. Whether a bias is created with respect to the mean distances migrated, by the apparent high rate of vulnerability of tagged fish to fishing pressure at the release site, was investigated.

Relative movements during the spring

TABLE 16. Frequency distributions of meristic numbers in fins of young white perch, *Roccus americanus*, of the 1953 year-class from the Patuxent River and Chesapeake Bay and its tributaries.

Locality[1]	Anal soft-rays						Pectoral fin rays							
	Number			N	$\bar{x}$	S.E.$_{\bar{x}}$	Number					N	$\bar{x}$	S.E.$_{\bar{x}}$
	8	9	10				14	15	16	17	18			
VI	—	17	7	24	9.29	0.095	—	8	13	3	—	24	15.79	0.134
IV	—	67	17	84	9.20	0.044	—	40	38	3	1	82	15.57	0.069
III	—	59	20	79	9.25	0.049	—	15	54	3	—	72	15.83	0.056
II	1	46	22	69	9.30	0.059	—	22	46	—	—	68	15.68	0.057
I	2	30	10	42	9.19	0.078	2	24	17	1	—	44	15.39	0.093
A	—	27	23	50	9.46	0.071	—	16	30	4	—	50	15.76	0.084
B	2	23	25	50	9.46	0.082	—	11	37	2	—	50	15.82	0.068
C	—	35	15	50	9.30	0.065	—	15	29	6	—	50	15.82	0.089
D	—	34	26	60	9.43	0.064	—	3	45	8	—	56	16.09	0.058
E	1	49	30	80	9.36	0.057	1	1	34	42	1	79	15.52	0.069
F	3	219	76	298	9.24	0.026	2	109	168	9	1	289	15.65	0.034
G	—	39	37	76	9.49	0.058	3	17	49	2	—	71	15.70	0.070
H	—	47	3	50	9.06	0.034	2	25	23	—	—	50	15.42	0.081

	Dorsal soft-ray							Character index							
	Number				N	$\bar{x}$	S.E.$_{\bar{x}}$	Number						N	$\bar{x}$	S.E.$_{\bar{x}}$
	10	11	12	13				34	35	36	37	38	39			
VI	—	4	20		24	11.80	0.078	—	3	4	10	7	—	24	36.88	0.202
IV	—	21	61	2	84	11.77	0.052	—	11	28	32	11	1	83	36.55	0.102
III	—	13	66	1	80	11.85	0.044	—	3	25	34	16	1	79	36.84	0.094
II	1	16	50	2	69	11.77	0.062	—	6	21	28	12	2	69	36.75	0.114
I	1	13	28	1	43	11.78	0.027	2	7	14	17	2	—	42	36.24	0.148
A	—	3	46	1	50	11.96	0.039	—	—	11	21	16	2	50	37.18	0.117
B	—	4	46	—	50	11.92	0.039	—	—	10	22	15	3	50	37.22	0.119
C	—	9	41	—	50	11.82	0.055	—	—	16	20	14	—	50	36.96	0.111
D	—	3	56	1	60	11.97	0.033	—	1	1	26	25	3	56	37.50	0.095
E	1	9	65	2	77	11.88	0.049	1	4	25	31	14	2	77	36.78	0.104
F	2	67	225	6	300	11.78	0.028	2	30	92	121	48	4	297	36.66	0.054
G	—	15	59	2	76	11.83	0.051	—	5	13	30	23	3	74	37.04	0.109
H	—	7	43	—	50	11.86	0.049	—	5	25	20	—	—	50	36·30	0 092

[1] VI = Patuxent River, zone 6: mouth of estuary.
IV = Patuxent River, zone 4: mid-estuary.
III = Patuxent River, zone 3: between Patuxent River bridge and Lower Marlboro.
II = Patuxent River, zone 2: Lower Marlboro to Lyons Creek.
I = Patuxent River, zone 1: Lyons Creek to Priests Bridge.
A = Upper Chesapeake Bay, western shore.
B = Chester River, lower estuary.
C = Chesapeake Bay, off Rock Hall.
D = Chesapeake and Ohio Canal in upper Potomac River at Big Pool.
E = Potomac River, mid-estuary.
F = Patuxent River, zones I–VI.
G = Nanticoke River, lower estuary.
H = James River, Virginia, in mid-estuary.

spawning period.—Many of the white perch tagged in spring during the height of the spawning season, as determined from the condition of gonads, were recaptured soon after tagging. This resulted in a shorter distance than the fish might normally have traveled had it not been recaptured so soon by the commercial fishery. A comparison was made of the relative movements of these fish of less than 10 miles and greater than 10 miles for 0–90, 91–180, 181–270, and 271-plus days free. For female white perch free 90 days or less, somewhat more than half of the recoveries were taken within 10 miles of the point of release. The balance of less than one half of the females were taken more than 10 miles from the tagging site, indicating that they are able to make relatively long-range and unencumbered movements. These proportions indicate that although the other half, all of which were in spawning condition, were recaptured within 10 miles of the tagging site, the results do not mean that they too had not or would not undertake long-range movements. Evidence will be introduced in the section on reproduction to show that females in Zone V of relatively high brackish water did not spawn in this area; therefore, as a species that spawns in tidal freshwater or slightly brackish water, they would have had to

TABLE 17. Recoveries of tagged white perch, *Roccus americanus*, by sex and by zones in which they were marked and recovered in the Patuxent estuary, Maryland.

Zones of recovery	Sex[1]	Zones of tagging							Totals	Grand total
		I	II	III	IV	V	VI	VII		
I	FF	34	—	—	—	1	—	—	35	
	MM	57	1	—	—	1	—	—	59	
	??	1	—	—	—	—	—	—	1	95
II	FF	3	1	—	—	1	—	—	5	
	MM	3	—	2	—	1	—	—	6	
	??	—	—	—	—	—	—	—	—	11
III	FF	21	—	6	—	19	3	—	49	
	MM	38	—	4	—	6	—	—	48	
	??	—	—	2	3	5	1	—	11	108
IV	FF	5	—	1	—	10	—	—	16	
	MM	11	—	—	—	2	—	—	13	
	??	—	—	—	—	2	—	—	2	31
V	FF	4	—	—	—	33	—	—	37	
	MM	8	—	—	—	9	—	—	17	
	??	1	—	—	—	3	2	—	6	60
VI	FF	—	—	—	—	—	2	—	2	
	MM	3	—	—	—	1	2	—	6	
	??	—	—	—	—	—	6	—	6	14
VII	FF	—	—	—	—	—	2	2	4	
	MM	—	—	—	—	—	1	—	1	
	??	—	—	—	—	—	—	—	—	5
Totals	FF	67	1	7	—	64	7	2	148	
	MM	120	1	6	—	20	3	—	150	
	??	2	—	2	3	10	9	—	26	324
Grand total[2]		189	2	15	3	94	19	2	324	—
Length of zone (miles)		16	8	11	13	8	8	—	—	61
Number of fish tagged		1707	66	112	94	776	245	24	3024	—

[1] FF = females; MM = males; ?? = unsexed fish.
[2] Contains a few fish of unknown sex.

TABLE 18. Distances traveled in miles by male and female white perch, *Roccus americanus*, largely in the Patuxent River as indicated by recaptured fish tagged during all seasons combined.

Miles midpoint	All zones upstream			All zones downstream			Total[1] recaptured	Per cent recaptured
	Sex[2]							
	FF	MM	T[1]	FF	MM	T[1]		
2.5	17	36	64	47	36	86	150	46.3
7.5	7	2	9	12	4	16	25	7.7
12.5	4	1	9	2	1	3	12	3.7
17.5	2	4	9	—	—	—	9	2.8
22.5	17	6	26	—	—	—	26	8.0
27.5	3	—	4	16	33	49	53	16.4
32.5	1	2	3	8	8	16	19	5.9
37.5	1	—	1	3	6	9	10	3.1
42.5	—	—	—	1	1	2	2	0.6
47.5	1	—	1	3	7	11	12	3.7
52.5	—	—	—	1	2	3	3	0.9
57.5	—	—	—	—	—	—	—	—
62.5	1	—	1	—	1	1	2	0.6
67.5	—	—	—	—	—	—	—	—
72.5	1	—	1	—	—	—	1	0.3
Total recaptured	55	51	128	93	99	196	324	100.0

[1] Contains some fish of unknown sex.
[2] FF = Females; MM = Males.

travel far upstream to deposit their eggs. Male white perch free 90 days or less generally showed the same type of movements as the females.

Among the females free between 91 and 180 days, the same general proportions are observed, although the males reverse the tendency, i.e., more than one half were recaptured over 10 miles from the tagging site. The balance of somewhat over one third of the males were taken less than 10 miles from the tagging site. The data is too fragmentary to generalize on the results of the distances traveled by the two sexes free for 181–270 days and 270 days or more, although in the latter freedom interval, all the males and females had traveled beyond 10 miles of the tagging site. These results indicate that the rate of movement between zones is not greatly encumbered by a high fishing intensity before the fish have had sufficient time to recover from the tagging procedure. The mean distance traversed by spring-tagged fish, however, is apparently underestimated by their premature capture on the tagging site.

Relative movements during summer, fall and winter:—The recaptures from white perch tagged in spring months are in contrast to the results of summer, fall and winter marking (see Table 20). Since few recaptured fish were sexed when tagged during those months, the 36 returns (comprising 9 females, 6 males, and 21 fish of unknown sex) are combined. The returns show that during the three to six month period following tagging, well over three quarters of the fish were taken in areas less than 10 miles from the tagging site. This fact indicates that white perch apparently do not undertake migrations of the

TABLE 19. Distances traveled in miles by recaptured white perch, *Roccus americanus*, after being tagged in spring months in the Patuxent River, 1952–54.

Midpoint distance in miles	Tagged in Zone I									Tagged in Zone 5								
	Days free[2]									Days free[2]								
	0–1		1–90		90–180		180 +		T	0–1		1–90		90–180		180 +		T
	FF	MM	FF	MM	FF	MM	FF	MM		FF	MM	FF	MM	FF	MM	FF	MM	
2.5	30	49	4	11[1]	—	—	—	—	94	—	—	19	5	5	3	1	—	33
7.5	—	—	3	2	—	—	—	—	5	—	—	10	1	2	1	—	—	14
12.5	—	—	—	1	—	—	—	—	1	—	—	7[1]	1	—	1	—	—	9
17.5	—	—	—	—	—	—	—	—	—	1	—	1[1]	1	1	—	—	1	5
22.5	—	—	—	—	—	—	—	—	—	—	—	14	4	—	—	3[1]	1	22
27.5	—	1	14	29	—	—	1	3	48	—	—	—	—	—	—	—	—	—
32.5	—	—	2	—	3	4	3	4	16	—	—	2	—	—	—	—	1	3
37.5	—	—	3	3	—	—	—	3	9	—	—	—	—	—	—	—	—	—
42.5	—	—	1	1	—	—	—	—	2	—	—	—	—	—	—	—	—	—
47.5	—	—	3[1]	4	—	3	—	—	10	—	—	—	—	—	—	1	—	1
52.5	—	—	1	2	—	—	—	—	3	—	—	—	—	—	—	—	—	—
57.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
62.5	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Totals	30	50	31	54	3	7	4	10	189	1	—	53	12	8	5	5	3	87
Mean distance traveled in miles	2.5	2.6	26.9	25.8	32.5	37.8	31.2	32.5	17.2	17.5	—	11.5	11.2	5.6	5.5	23.5	24.0	11.4

[1] Also contains one fish of unknown sex.
[2] Seasons of days free of spring-tagged fish—(a) 0–1—Spring; (b) 1–90—Spring and early summer; (c) 90–180—Summer and fall; d) 180 +—fall, winter and spring.

same magnitude as fish tagged in spring during these periods. Among the many recaptures tagged in summer and fall and free less than six months, most of them have been taken but a few miles from their tagging site. The reason why most of the fish free between 181–270 days in spring and 90–180 days in fall were caught more than 10 miles from their tagging sites is that about nine and six months following summer and fall tagging, respectively, during the spring months, these fish resume their large-scale spawning migrations, hence their patterns of movement would be similar to that of spring-tagged fish in the 1–90 day free category.

Distances traveled by spring-tagged fish:—The mean distance in miles traveled by all white perch tagged during spring months was 15.6, with upper ranges of 45 miles or more (see Table 19). There was considerable variation, however, in the distances traveled by white perch, depending on the zone in which they were tagged. For example, among fish tagged in Zone I, and free between 1–90 days (Table 19), male and female fish averaged 26.9 and 28.8 miles, respectively, from the site of tagging. Some fish traveled downstream as much as 45 and 50 miles. The differences in distances traveled by the two sexes are not statistically significant. If, on the other hand, recoveries made on the same day of tagging are included in the calculation of these estimates, then the estimate of mean distance traveled is lower. This is indicated by the mean of 17.2 miles for both sexes recaptured throughout the year. It is important to emphasize, at this point, that there are apparently no resident population of white perch in the upper part of Zone I. This is indicated by failure to catch the fish by repeated seining throughout the area in summer and fall, by the lack of a heavy fishery in this zone for this species, and as a consequence, a lack of tag returns from this area except in spring. Curtailed fishing for other species of fish, however, continues in this area during the summer months.

Zone I is an area subject to a high density of spawning fish and intensive fishing pressure for white perch and other anadromous fish only during the spring season. Soon after tagging operations began at this site, it was apparent that many tag recoveries would be made in the immediate vicinity. Records were kept of each recaptured fish with regard to distance in feet traveled by each sex either downstream or upstream.

TABLE 20. Distances traveled in miles by recaptured white perch, *Roccus americanus*, after being tagged in summer and fall months in the Patuxent River, 1952–1955.

Summer[1]	Distance in miles (Midpoints)						Totals
Days free[2]	2.5	7.5	12.5	17.5	22.5	27.5	
0–90	10	—	—	—	—	—	10
90–180	1	—	—	—	—	—	1
180–270	1	—	3	1	2	1	9
271 +	1	—	—	1	1	—	3
Total	13	—	3	2	3	1	22
Fall[3]							
0–90	4	2	—	—	—	—	6
90–180	4	—	—	1	1	—	6
180–270	—	—	—	—	—	—	—
271 +	1	—	—	—	—	—	1
Total	9	2	—	1	1	—	13

[1] Sex of fish unknown.

[2] Season of days free—(a) 0–90—summer; (b) 90–180—fall; (c) 180–270—winter; and (d) 271 +—spring.

[3] Sex of fish consisted of 7 females and 6 males.

Generally most of the recaptures clustered around the site of tagging, although some fish were taken at much greater distances than the mode at about 40–60 feet. The lack of greater numbers of recaptures farther up- and downstream can be attributed to the decline in fishing intensity in those areas, and to the reluctance of fishermen to bring tags to the tagging site or send information by mail. Virtually all of these recaptures were made on the same day of tagging, although some fish were recaptured at the tagging site as long as a week later, and one was taken 13 days after tagging a short distance from the tagging site.

The mean distance in miles (11.4) traveled by all white perch in Zone V was less than that of both the male and female fish from Zone I, although none traveled over 50 miles from the tagging site. Among fish free 1–90 days (see Table 19), male and female white perch, averaged 11.5 and 11.2 miles, respectively, with considerable distances traveled on either side of the mean. Here again the differences in distances traveled between the two sexes are not statistically significant. For fish free longer than 90 days the returns are not complete enough to generalize on the results of distances traveled. There is a seasonal variation as mentioned above. The data for recaptures of fish tagged in Zone VI is too fragmentary for more than a passing comment. The mean distances traveled by males and females in this zone are somewhat midway between the means calculated for fish from Zone I and V.

Distances traveled by summer and fall tagged fish:—The mean distance in miles traveled by all white perch tagged during summer and fall months is 7.9 miles, with variation around this mean depending on days free (Table 20). This estimate is apparently high since it includes fish that usually begin their extensive spawning movements nine and six months later, depending on whether they were tagged in summer or fall. Thus the summer-tagged fish that were recaptured in the 90–180 days free category, would be traveling distances comparable or close to the mean values cited for spring-tagged fish. No comments can be made about sexual differences in summer and fall movements, since most of these fish could not be reliably sexed when tagged.

Comparison of tagged sample to recaptured sample:—The relationship of the sizes of the recaptured to the tagged sample must be close in order to assess the reliability of the returns by commercial and sport fishing. Fig. 16 shows this size relationship at tagging for both sexes by two different types of gear in two ecological Zones in the Patuxent River. As can be seen by the significance diagram comparisons of the means, various parameters of the sizes of all tagged and recaptured male and female white perch overlap for each of the two groups compared, except for female white perch tagged in Zone I. The latter, however, is of little practical importance, although it is probably due to selectivity of gear for the larger females. In general, it appears that the recaptured fish were representative of the tagged fish. Fish tagged in Zone V were of the same general sizes as those taken in the spring period by the commercial fishery, whereas those from Zone I were not. As can be seen in the figure, the mode of both sexes is considerably below the 8-inch minimum

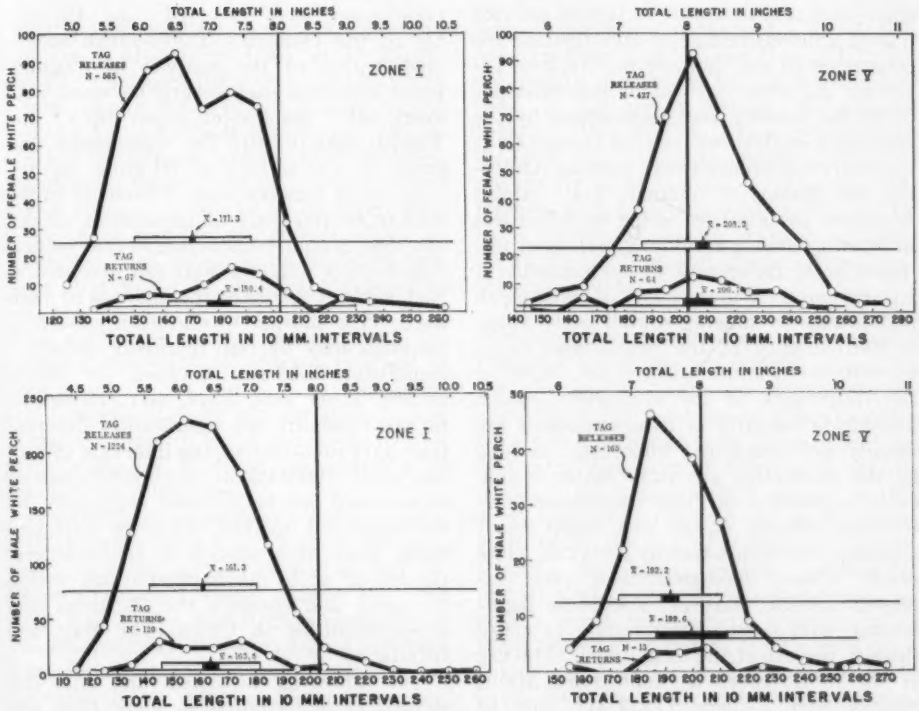

Fig. 16.—Comparison of size frequency distributions of white perch, *Roccus americanus*, tagged and released in the tidal freshwater spawning area (Zone I) and the lower brackish feeding area (Zone V) with marked recaptures to show variation in sizes between releases and returns. Measurements of recaptures are based on data recorded at the time of release of the tagged fish.

size, although all of these sizes were being caught by unlicensed commercial and sports fishermen in Zone I. The tagging in Zone I was conducted with the aid of the same gear used by unlicensed netters, and occasionally catches by these fishermen were tagged. It may be assumed, therefore, that the sizes of fish tagged in Zone I are more nearly related to the mean sizes of smaller, somewhat younger fish occupying the area for spawning, while those tagged in Zone V represented the older larger fish selected by mesh size of experimental trap nets that was comparable or slightly less than that used by commercial netters. It is believed that smaller fish were not adequately sampled for tagging purposes in Zone V as they were in Zone I.

Local Populations Based on Meristic Counts

The objectives of the meristic study of white perch populations, which serves to complement the tagging study, were to determine:

(1) the occurrence of discrete local populations based on morphological characters within and outside the Patuxent River;

(2) the variation in meristic characters within and between samples of white perch populations from different localities; and

(3) the relationship of these results with those based on tagging.

Tracing the migration of white perch by

the release and recapture of tagged individuals is a direct method of investigating the occurrence of one or more populations. Inferring the occurrence of or non-existence of mixing between such populations by the statistical analysis of meristic characters is the indirect approach to the question. Different populations of animals may exhibit structural peculiarities owing to differences in heredity arising from long periods of isolation or to differences in environment. A natural corollary to the study of white perch populations by tagging studies is the study of individuality of the populations based on certain structural differences. Whether the differences in the characters chosen are due to heredity or to environment are usually not considered important, as long as the characters are fully stable within each population so that significant differences indicate no, or very slight intermingling, between adjacent stocks of white perch. Fishery biologists, who have employed meristic features to separate populations, have been indiscriminate in many cases in the use of the term "race." The use of the term "race" as defined by Mayr, Linsley and Usinger (1953:31) will be avoided here, and in its place "subpopulation" is used for the discrete groups of white perch from different areas in the Patuxent River and Chesapeake Bay (Marr, 1957:1).

Although the distributions of each of the characters (Table 16) are primarily discrete, *t*-tests and other normal distribution tests are frequently used for binomial distributions (Snedecor, 1956:475–7). Accordingly, the statistical treatment of this data consisted of three phases, ranging from a simplified to a critical approach: (1) construction of Hubbs and Hubbs (1953:49–57) significance diagrams (originally modified from Dice and Leraas, 1936:13) with a cognizance of their conservative use expressed by Simpson and Roe (1939:192–4) and Simpson, et al (1960:351–6), in order to see gross differences between the confidence intervals (two standard errors on either side of the means) of the populations; (2) use of *t*-tests where the statistical significance between only two or three populations were involved; and (3) the use of the Duncan multiple-range test, a modification of the analysis of variance which compares each geographic mean with every other geographic mean (Steel and Torrie, 1960:107–9). The significance diagrams proved to be a useful guide for distinguishing between wide differences in the confidence intervals of population means, but close comparisons of means that seemed significantly different were not accepted as such without *t*-tests or the analysis of variance. This caution was necessary because intervals may overlap markedly despite a significant difference between the means at the 5 per cent level, and conversely, means which are not significantly different may have non-overlapping intervals (Simpson, et al, 1960:352–3). Such difficulties as these could not be assessed accurately by the graphical method. Duncan multiple-range tests were applied to the character indices of white perch populations within the river and between the Patuxent and seven localities in Chesapeake Bay and tributaries.

The spines in the dorsal and anal fins showed little variation in more than 600 specimens counted. All variants were from different collections and localities. The first dorsal had 9 spines except in 20 fish, where one had 7, nine had 8, and eleven fish had 10. The second dorsal fin consistently had one spine. The anal fin consistently had three spines. Frequency distributions, with means, standard deviations, and twice the standard errors of the mean, were plotted in significance diagrams for the dorsal, anal and pectoral fins in order to assess broad differences between means.

Dorsal soft-ray variations:—The dorsal soft-rays, ranging from 10 to 13 rays, are relatively variable in samples within and between drainage systems (Table 16). The most frequent counts were usually 12, followed by 11. A few Patuxent River fish possessed 10, while none of the fish examined from Chesapeake Bay and its tributaries were found to have this number. About the same number of fish within the Patuxent River estuary and in Chesapeake Bay and its tributaries had 13 rays. Signifi-

cance diagrams of dorsal soft-ray means of samples of white perch taken in the Patuxent River estuary from tidal freshwater in Zone I to salt water of the estuary mouth in Zone VI, indicate that there are no significant differences between these samples. Significance diagrams of the tabular data of dorsal soft-ray means of white perch from Chesapeake Bay and tributaries, which include the mean for all Patuxent River fish, show that there are significant differences between certain samples. The lack of a cline within the Chesapeake Bay, i.e., low counts in the south following a gradient to high counts in the north, is evident. Generally speaking, however, variation among dorsal soft rays is not high, hence it is of little value in showing phenotypical or genotypical differences.

Anal soft-ray variation:—The anal soft-rays, ranging from 8 to 10 rays, are relatively variable in samples within and between drainage systems (Table 16). The mode was 9 rays, and 10 rays occurred often. Infrequently, fish with 8 anal soft-rays were found among the intra- and extra-Patuxent River samples. Significance diagrams of the tabular data of anal soft-ray means of white perch taken in the Patuxent River estuary indicate that there are no statistically significant differences between these samples. Analysis of the data shows that statistically significant differences exist between various samples from Chesapeake Bay and tributaries, and that at least three of these samples are different from the combined Patuxent River sample. The variation among anal soft-rays, however, is not great, hence this meristic character alone is of little value in separating populations.

Pectoral ray variation:—The pectoral ray counts as shown in Table 16 indicate that this meristic character gives the best separation of any single character. The mode for all samples was 16 rays, with 15 rays occurring frequently. Occasionally, white perch with 17 rays, and very few with 13 and 18 rays, were counted. Significance diagrams of the tabular data of pectoral ray means of fish taken in the Patuxent River demonstrated that significant differences occurred among the samples of fish between Zone I and Zones II and III, but an analysis of variance of this data showed them to be non-significant. It appears, therefore, that this fin is more plastic than the other two, and that phenotypically, it is potentially of some value in observing differences in local populations. Zone I and IV have the lowest means, thereby conforming to the low means of the dorsal and anal soft-ray counts.

Among fish from Chesapeake Bay and tributaries, compared with the combined Patuxent River estuary sample, it appears that the sample means are extremely variable (Table 16). Low means generally agree with the low means from dorsal and anal soft rays, with several differences, but the pectoral fin counts varied largely in the same way as the dorsal and anal counts. Here again, the lack of a cline is indicated. Pectoral fin counts exhibit considerable variation when compared to dorsal and anal counts, hence this meristic character is of importance in separating local populations. Combined with dorsal and anal counts to form the "character index," they proved of considerable value in separating subpopulations.

Variation in character index:—The character index is the total value obtained when the soft-rays of the dorsal, anal, and pectoral fins are added for each white perch. Table 16 shows the distribution of counts of the character index for fish samples from within and outside the Patuxent River estuary. The mode was 37 for all samples, with 36 and 38 occurring frequently. Fish with 35 occurred infrequently, while those with 34 and 39 were very rare. An analysis of variance of character indices of the Patuxent River samples indicate that the differences in the means of the samples from the various Zones were not statistically significant, although Zone I had a considerably lower mean than all the other zones. Where the means of dorsal and anal soft rays were relatively constant, it is obvious that the pectoral rays contributed to the generally variable nature of the character index among the Patuxent River sample.

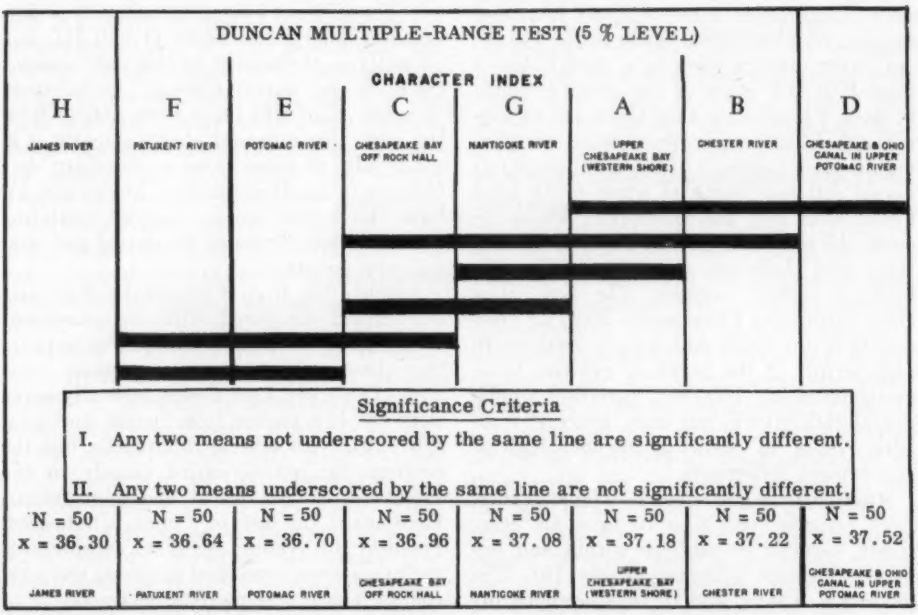
DUNCAN MULTIPLE-RANGE TEST (5 % LEVEL)
CHARACTER INDEX
H
JAMES RIVER
F
PATUXENT RIVER
E
POTOMAC RIVER
C
CHESAPEAKE BAY OFF ROCK HALL
G
NANTICOKE RIVER
A
UPPER CHESAPEAKE BAY (WESTERN SHORE)
B
CHESTER RIVER
D
CHESAPEAKE & OHIO CANAL IN UPPER POTOMAC RIVER
Significance Criteria
I. Any two means not underscored by the same line are significantly different.
II. Any two means underscored by the same line are not significantly different.
N = 50 x = 36.30 JAMES RIVER
N = 50 x = 36.64 PATUXENT RIVER
N = 50 x = 36.70 POTOMAC RIVER
N = 50 x = 36.96 CHESAPEAKE BAY OFF ROCK HALL
N = 50 x = 37.08 NANTICOKE RIVER
N = 50 x = 37.18 UPPER CHESAPEAKE BAY (WESTERN SHORE)
N = 50 x = 37.22 CHESTER RIVER
N = 50 x = 37.52 CHESAPEAKE & OHIO CANAL IN UPPER POTOMAC RIVER

Fig. 17.—Graphical representation of the Duncan multiple-range test of the differences between the means of character (meristic) indices of white perch, *Roccus americanus*, taken from the Patuxent River and seven other localities in Chesapeake Bay and its tributaries. The means of the localities are ranked from the smallest (James R.) to the largest (Chesapeake and Ohio Canal). The range test calls for a set of significant differences of increasing size, the size to depend upon the closeness of the means after ranking, with the smallest value for adjacent means and the largest for the extremes. The James River sample is significantly differentiated from all other samples. Data in this graph are based on Table 16, except that samples containing more than 50 individuals were sub-sampled by the use of the table of random numbers in order to produce equal sample sizes (N—50) for each locality in the test.

Among fish from Chesapeake Bay and tributaries, compared with the combined Patuxent River estuary sample, the character index has varied in the same general way as the pectoral counts. In general, the character index does not have increased value over the pectoral ray counts. Also, no cline was evident, as in the individual fin counts. Generally, the samples having the low mean and high mean counts are similar to the pectoral counts. A Duncan multiple-range test indicated that statistically significant differences existed between the James River and all other localities, and the Patuxent River and other areas. The results of the range test, which is a test of the homogeneity of the sample of means for the size of sample and one that uses range as a test criterion, are shown in Fig. 17.

Reproduction

Reproduction is basically concerned with the number of eggs produced and larval hatching, recruitment to the population, and other such factors. In most fish studies it usually refers to size and age at sexual maturity, spawning cycle, spawning area and season, development of gonads, fecundity, and the development of eggs and larvae. Certain basic questions were necessary before a complete detailed study of white perch reproduction could be undertaken. These questions became the primary objectives of this aspect of the study. They are:

(1) When and where do white perch spawn in the Patuxent River?
(2) What is the duration of spawning and how frequently do they spawn?
(3) At what size and age does spawning first begin in the two sexes?

Some investigations were undertaken to determine fecundity of females at different sizes and ages, but the problems inherent in precise estimation prevented completion of this phase of the study. The study of the eggs and larvae was carried out in great detail from material reared in the laboratory from adult white perch captured in the field, but this aspect of the study, although generally complete, is so specialized that it is left out of this report (see brief summary by Mansueti and Mansueti, 1955:1, 2–3). Results of the gross study of ovaries and early developmental stages of eggs and larvae, nevertheless, were necessary for the interpretation of the data on reproduction included in this study.

Female white perch are oviparous and fertilization of eggs is external as with most teleost fishes. No external characteristics have been found that help to differentiate between the two sexes, except during the spawning season. At that time, the sex of mature white perch is determined by applying pressure to the abdomen and noting the sexual products forced from the urogenital aperture. Males are immediately recognizable by the flow of white milt from the opening when abdominal pressure is exerted. They differ markedly from females as far as gonad maturation is concerned since they are capable of exuding sperm from late fall to the end of spawning in May. There is no evidence, however, that they voluntarily emit milt before spring. Females are recognized, if gravid, by their widely distended abdomens, by the loss of eggs, if ripe, when light pressure is exerted, or by their lean appearance, collapsed abdomens, and often by the expression of a few eggs when heavy abdominal pressure is applied if the fish is spent. Individual females are ripe for a short time, probably about a week, during April or May. Immature males and females are not encountered on the spawning grounds, so that collections for this group of fish were made in areas below Zone III in the Patuxent.

Collection of samples during all seasons indicated that developmental stages in the gonads of females were clearly marked. Since they were present at one time or another during the fishing season, they were distinguished by gross observation as follows:

A—Immature—Ovaries very small and string-like, and characterized by very little thickness in diameter, a pink color, and somewhat gelatinous appearance. These were not difficult to recognize at the peak of spawning by adults. Ovary diameter less than 0.25 mm (observed during first two or three summers of life).

B—Mature—Developing. Ovaries enlarging, becoming yellowish in color and granular in consistency, full of developing eggs that can be distinguished by direct observation. Diameters range from 0.30–0.70 mm (July–February).

C—Mature—Gravid. Ovaries very full of yellowish granular eggs that are partly translucent. Ova can be extruded from the oviduct by exerting considerable pressure. Diameters range from 0.65–0.75 mm (February–April).

D—Mature—Spawning-ripe. Ovaries very full of translucent mature ova. Eggs will run under a slight pressure. Diameters range from 0.75–0.80 mm (April–May).

E—Mature—Partly-spent. Ovaries somewhat flaccid and convoluted, with a variable number of eggs left. Ovarian membrane somewhat vascular, (April–May).

F—Mature—Spent. Ovaries flaccid, few translucent eggs left. Ovarian membrane very vascular, sac-like, or bloodshot. (May–June).

G—Mature—Resting. Ovaries becoming firm, and characterized by a relatively thick diameter. No eggs discernible to the naked eye, color pinkish, texture gelatinous. (June–July).

Among males the minuteness of even

the mature spermatozoa rendered the classification of their developmental stages exceedingly difficult. Only five distinctions were made for the males:

A—Immature. Testes very small, string-like, dull opaque in color. These were not hard to recognize in young that were taken and compared with testes of adults during the spawning period (Observed during first two summers of life).

B—Mature—Latent. Testes white, firm in texture, enlarging, but milt not running. (July–October).

C—Mature—Spawning-ripe. Testes white, enlarged, less firm in texture, and if compressed the white milt generally comes through the urogenital pore. (October–May).

D—Partly-spent. Testes whitish, somewhat flaccid and convoluted, with free flow of milt. (April–May).

E—Spent. Testes brownish white, flaccid and convoluted, with no flow of white milt upon compression. (April–early June).

TABLE 21. Condition of ovaries of sexually mature female white perch, *Roccus americanus*, examined on one of the spawning grounds of the Patuxent River at Queen Annes Bridge in spring, 1953.

Data	Mean water temp.[1]		Mature gravid		Mature ripe		Mature partly spent		Mature spent		Total examined
	C°	F°	No.	%	No.	%	No.	%	No.	%	
March 30	8.3	47	8	100.0	—	—	—	—	—	—	8
April 3	12.2	54	12	85.7	2	14.3	—	—	—	—	14
April 11	15.0	59	16	69.6	5	21.8	2	8.6	—	—	23
April 19	9.4	49	8	25.8	11	35.5	9	29.0	3	9.7	31
April 27	12.2	54	18	18.0	35	35.0	40	40.0	7	7.0	100
May 3	16.1	61	2	4.2	6	12.5	8	16.7	32	66.6	48
May 8	18.9	66	1	3.7	3	11.1	4	14.8	19	70.4	27
May 10	18.9	66	0	0	9	23.7	2	5.3	27	71.0	38
May 15	21.7	71	0	0	0	0	0	0	6	100.0	6
May 19	20.0	68	0	0	0	0	0	0	5	100.0	5
May 26	17.2	63	0	0	0	0	0	0	2	100.0	2
June 3	17.5	63	0	0	0	0	0	0	0	0	0
Total	—	—	65	—	71	—	65	—	101	—	302

[1] Taken every hour with a portable thermometer during the survey at this site.

TABLE 22. Condition of testes of sexually mature male white perch, *Roccus americanus*, examined on one of the spawning grounds of the Patuxent River at Queen Annes Bridge in spring, 1953.

Date	Mean water temp.[2]		Mature latent		Mature ripe		Mature partly spent		Mature spent		Total examined
	C°	F°	N	%	N	%	N	%	N	%	
March 30	8.3	47	0	0	3	100	0	0	0	0	3
April 3	12.2	54	0	0	7	100	0	0	0	0	7
April 11	15.0	59	0	0	25	92.6	2	7.4	0	0	27
April 19	9.4	49	0	0	63	94.0	3	4.5	1	1.5	67
April 27	12.2	54	1[1]	0.7	127	77.4	24	14.6	12	7.3	164
May 3	16.1	61	0	0	21	34.4	32	52.5	8	13.1	61
May 8	18.9	66	0	0	8	29.6	8	29.6	11	40.8	27
May 10	18.9	66	0	0	16	25.4	22	34.9	25	39.7	63
May 15	21.7	71	0	0	0	0	2	18.2	9	81.8	11
May 19	20.0	68	0	0	2	25.0	2	25.0	4	50.0	8
May 26	17.2	63	0	0	0	0	1	33.3	2	66.7	3
June 3	17.5	63	0	0	0	0	0	0	0	0	0
Total	—	—	1	—	272	—	96	—	72	—	441

[1] There is some reason to believe that this small male in the 120–130 mm. group was immature.

[2] Taken every hour with a portable thermometer during the survey at this site.

During tagging and field operations in the spring months, a detailed record was maintained concerning the sexual condition of all fish handled or observed in the field. Collections of fish made in all the remaining seasons yielded further information that was essential in determining age, size and period of spawning. A study of the condition of gonads in relation to time of collection was utilized in further ascertaining the spawning period. Plankton collections were made with a fine-mesh tow-net from late February to June in areas where white perch were believed to spawn. These collections were necessary to corroborate time and location of spawning in areas visited by sexually mature fish.

Season and location of spawning:—The spawning season was determined by combining three sets of data: (1) examination of condition and development of the gonads; (2) presence of eggs and larvae in plankton collections; and (3) movement and activity of fish on a seasonal basis. Monthly collections of ovaries were grossly inspected and the stage of development was recorded. These observations indicate that the gonads ripened to a spawning condition during April and May. The data indicated also that the white perch spawned once a year. Table 21 indicates in more detail the stages of ovary development in relation to various dates and water temperatures. The same information for males is given in Table 22.

Early in April the spawning-ripe fish exceeded the gravid fish in numbers. Spawning-ripe fish were found from early April to early May, and percentage plot of this group indicates a spawning curve for the white perch at this site in the Patuxent River in April, 1953. Partly spent fish were found from mid-April to mid-May, while completely spent females were found from late April to the end of May.

A preliminary separation and identification of the white perch eggs and larvae from the plankton collection indicated that ova were found in the same general area at the same time that spawning-ripe and partly spent females were taken. Positive identification of eggs and larvae was assured by stripping females of ova and fertilizing them with the milt from males and rearing them in the laboratory (Mansueti and Mansueti, 1955:1, 2–3). Eggs and early prolarvae were not taken before early April nor after early June. Whenever samples were taken from commercial fishermen, an attempt was made to locate spawning-ripe females among the catch. This stage of development was not found except in catches taken in fresh water or slightly brackish water above Zone III in the upper Patuxent River. Wherever such fish were observed, eggs and larvae could be collected in adjacent waters.

Tagging indicated most fish that were marked while in spawning condition from Zones VI to III were recaptured at some point upstream from the tagging site. Such upstream movements occurred only during the spring months. In addition to the tagging studies, substantial evidence that there were large-scale migrations upstream was gathered from the commercial fisheries. In almost all such cases the fish were gravid, indicating that a suitable spawning area upstream was apparently a primary motivation in their movements.

Observations on spawning-ripe females and the collection of eggs and larvae delimited the spawning grounds of white perch to the upper tidal, largely, freshwater area of the Patuxent River. Eggs and larvae were discovered in plankton collections from early April to the end of May from Queen Annes Bridge to Lower Marlboro, a distance of about 22 miles downstream. Larvae were taken at stations a few miles below Lower Marlboro, as well as at the mouth of Western Branch and Hall Creek. General condition of spawning sites varied from a high velocity of water flow at the narrow portion of the River at Queen Annes Bridge to a slow moving broad tidal river further downstream. Almost all eggs collected in plankton samples were found adhering to debris. Laboratory studies showed that upon being exuded and fertilized the ova sink to the bottom and stick firmly to the first object with which contact is made.

Sex ratios in spawning and non-spawning areas:—Sex ratios on the spawning grounds were markedly unbalanced. Of 1789 adult white perch captured in the spawning grounds in the Patuxent River at Queen Annes Bridge in Zone I, 68.4 per cent were males. The number of males captured varied with the progress of the spawning season (Table 22). Most of the samples during the early part of the run consisted of males and numerically they dominated the spawning area during spring. They were the first to arrive in this area, but a small but increasing number of females apparently entered the area shortly afterwards until the latter part of April when females reached a peak of over 35 per cent. This period apparently coincided with the peak of the occurrence of the spawning-ripe stage of females. The evidence generally shows that males usually preceded the females by a few days on the spring migration, and that the reverse, i.e., females leave the area before males, took place toward the close of the run.

Sex ratios of fish taken by trap nets in the lower Patuxent estuary at almost the same time as the fish taken on the spawning grounds showed the opposite condition. Of 787 adult fish caught for tagging in the brackish water feeding grounds near the junction of St. Leonards Creek with the Patuxent, 70.5 per cent were females. The percentage of females present varied somewhat with the progress of the spawning season (Table 23). There were somewhat fewer females at the beginning and end of the

TABLE 23. Percentages of sexually mature female white perch, *Roccus americanus*, taken at two widely separated areas in the Patuxent River, spring, 1953.

Date	Upper Patuxent estuary Zone I—Spawning area				Date	Lower Patuxent estuary Zone V—Feeding area			
	Female	Male	Total	Percentage of females		Female	Male	Total	Percentage of females
March 30	1	42	43	2.3	March 31	12	8	20	60.0
April 3	3	50	53	5.7	April 4	18	3	21	85.7
April 11	8	43	51	15.7	April 9	107	53	160	66.9
April 19	17	64	81	21.0	April 18	61	9	70	87.1
April 27	115	218	333	34.5	April 24	82	27	109	75.2
May 3	42	181	223	18.8	April 30	83	16	99	83.8
May 11	26	71	97	26.8	May 3	133	58	191	69.6
May 15	94	228	322	29.2	May 7	19	24	43	44.2
May 19	3	6	9	33.3	May 10	32	25	57	56.1
May 26	2	3	5	40.0	May 15	8	9	17	47.0
Totals	311	906	1217	25.6		555	232	787	70.5

period that coincided with the spawning period. Tagging studies showed that these fish migrated upstream, presumably to spawn, but only one of these tagged fish was ever recovered in the spawning site described above.

Spawning behavior:—A review of the literature indicates that the spawning behavior of white perch has never been observed. After ascending rivers and creeks they presumably spawn under banks of streams or under old trees and debris. Since the water is usually quite turbid in the spawning areas at Queen Annes Bridge it was extremely difficult to observe the courtship pattern. On one occasion when the water was relatively clear at dusk in April, 1953, an audible splashing revealed the presence of a school of white perch consisting of several large individuals, presumably females, being trailed by more than a dozen smaller fish, presumably males. A constant milling about of all the fish took place, followed by the females swimming to the surface and creating a disturbance. One of the large fish swimming along a horizontal path to the bottom left a barely distinct trail, indicating ovulation, and this was followed by prominent emission of white milt by males. Although the flow carried much of the milt downstream, some white perch eggs in the early cleavage stages, presumably from this spawning, were collected a short time later in the immediate area.

TABLE 24. Relationship of standard length of Patuxent River white perch, *Roccus americanus*, and proportion of sexually-mature fish, 1953–1954.

Standard length interval	Female		Male		Sexes combined	
	Total examined	Percentage mature	Total examined	Percentage mature	Total examined	Percentage mature
Less than 60 mm.	1	0	0	0	1	0
60–70	2	0	3	0	5	0
70–80	9	0	14	0	23	0
80–90	37	0	36	2.8	73	1.4
90–100	24	8.3	31	51.6	55	32.7
100–110	29	48.3	36	83.3	65	67.7
110–120	43	90.7	62	100.0	105	96.2
120–130	69	95.7	76	100.0	145	97.9
130–140	72	97.2	84	100.0	156	98.7
140–150	74	98.6	91	100.0	165	99.4
150–160	91	97.8	103	100.0	194	98.9
160–170	110	100.0	117	100.0	227	100.0
170 and over	175	100.0	165	100.0	340	100.0
Total	736		818		1554	

Sizes and age at maturity:—The size at maturity of white perch for both sexes is shown in Table 24. None of these fish were sexually mature under 80 mm standard length, while all were mature above 160 mm. In general the males mature earlier, beginning at 80 mm, than do the females, which begin to mature after they attain 90 mm. A convenient way to describe the length at sexual maturity is to determine the size at which 50 per cent of the animals have mature gonads. This is determined by plotting the data on arithmetic probability paper. The length at which 50 per cent of the males are sexually mature is 100.3 mm, and the length at which 50 per cent of the females are sexually mature is 105.5 mm.

The age at maturity of white perch is shown in Table 25. Males mature at an earlier age than females; all those examined in age group II and older were sexually mature. None of age group I, however, were sexually mature. Among the females, all were sexually mature from age group IV and older, but immature fish were found among the first three age groups. None, of course, were sexually mature in age group

TABLE 25. Relationship of age in years and standard length of Patuxent River white perch, *Roccus americanus*, and proportion of sexually mature fish, 1953–54.

Standard length intervals, mm	Age Groups															
	I				II				III				Total			
	Females		Males		Females		Males		Females		Males		Females		Males[2]	
	N	Per cent mature	N	Per cent mature	N	Per cent mature	N	Per cent mature	N	Per cent mature	N	Per cent mature	N	Per cent mature	N	Per cent mature
Less than 60 mm	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
60–70	2	0	3	0	0	0	0	0	0	0	0	0	2	0	3	0
70–80	8	0	14	0	1	0	0	0	0	0	0	0	9	0	14	0
80–90	33	0	35	0	4	0	1	100.0	0	0	0	0	37	0	36	2.7
90–100	15	0	15	0	8	25.0	5	100 0	1	0	0	0	24	8.3	20	25.0
100–110	9	0	6	0	9	66.6	15	100.0	11	72.7	16	100.0	29	48.3	21	71.4
110–120	1	0	0	0	10	80 0	16	100.0	32	96.9	29	100.0	43	90.7	16	100.0
120–130	0	0	3	0	12	83.3	14	100.0	57	98.2	24	100.0	69	95 7	17	82.4
130–140	0	0	0	0	12	83.3	14	100.0	38	97.4	33	100.0	50	96.0	14	100.0
140–150	0	0	0	0	4	100.0	2	100.0	38	97.4	23	100.0	42	97.6	2	100.0
150–160	0	0	0	0	3	66.0	1	100.0	28	96.4	30	100.0	31	93.5	1	100.0
160–170	0	0	0	0	1	100.0	6	100.0	13	100.0	4	100.0	14	100.0	6	100.0
170–180[1]	0	0	0	0	0	0	0	100.0	5	100.0	1	100.0	5	100.0	0	0
Total	69		76		64		74		223		160		356		150[2]	

[1] All females dissected above age group III and above 180 mm standard length (221 mm or 8.7 inches T.L.) were sexually mature.
[2] The total and percentages include age groups I and II only; all males dissected from age group III and above and those above 150 mm S.L. (184 mm or 7.2 inches T.L.) were sexually mature.

I. Within age groups II and III sexual maturity seemed to be related to size rather than age. For example, in both age groups, proportionately more fish are mature above 120 mm than below it. The bulk of the mature sample, nevertheless, is concentrated in age group III in these two groups.

MORTALITY

The age distribution existing in a randomly taken sample of a fish population can be used to estimate the survival rate of the population during successive years of life. In this study the annual probability of dying (usually referred to as annual mortality rate in the fisheries literature) and annual probability of survival (annual survival rate) are estimated from age frequencies in the catch by plotting the logarithms of frequencies against age and taking the slope of the resulting catch curve at successive ages, based on methods outlined by Ricker (1948:7–27) and Rounsefell and Everhart (1953:86–90). The probability of dying (q) is defined as the proportion of animals that died during some time interval out of a particular initial population. The probability of surviving (p) is the complement of the probability of dying. Thus, $p + q = 1$ and q can never be more than 1.

The calculation of the annual probability of dying by the use of age distribution is affected by three principal sources of error, one systematic and two random. Systematic error comes from the unequal vulnerability of fish of different ages to the fishing gear in use. A part of the samples used in this study were taken by gillnets, which are selective for size and hence by age, the remainder of the samples were taken by relatively unselective methods. It is believed that the best representation exists between age groups III and VIII. The sources of random error in estimating mortality from age frequencies include (a) ordinary sampling error and (b) error due to fluctuations in the supply of fish which are hatched in successive years, or which survive to become catchable size. Ordinary sampling error has been discussed in greater detail elsewhere, and efforts have been directed toward minimizing it. Error due to fluctuations in supply may also occur. Some idea of the size of these fluctuations may be seen in apparent fluctuations derived indirectly from the index of population density inversely correlated with first-year growth of 13 year-classes. Serious obstacles to the accurate estimation of probability of dying were minimized by combining catches taken in successive years, or by smoothing,

as well as possible, a graph obtained for successive ages as well as possible to reduce variations due to uneven recruitment. Fig. 18 shows that recruitment was fairly uniform, for the curve is relatively smooth for the two sexes individually and combined.

As can be seen in Table 15, the modal age in the catch is practically always greater than age-group I, and in most cases above age groups II and III. Obviously no information about annual probability of survival is to be obtained from fish younger than the modal age. Information derived from ages close to the mode apparently are not as reliable because these regions correspond to the ascending limb and dome of the catch curve. Beyond the right side of the mode of a catch curve there is usually no direct evidence that vulnerability to selective gear continues to increase or not. Among old fish several adjacent ages were taken in a single size of gill net without any pronounced selection for size. This factor helps to minimize this source of error.

TABLE 26. Computed annual probability of dying based on age frequencies of white perch, *Roccus americanus*, from the Patuxent River, Maryland.

Year of collection	Sex[1]	Annual probability of dying	
		Unweighted	Weighted
1948	Females	0.46	0.63
	Males	0.44	0.50
	Combined	0.48	0.44
1949	Females	0.38	0.37
	Males	0.37	0.38
	Combined	0.44	0.42
1950	Females	0.42	0.44
	Males	0.38	0.36
	Combined	0.48	0.41
1951	Females	—	—
	Males	0.39	0.34
	Combined	0.46	0.42
1952	Females	—	—
	Males	—	—
	Combined	0.55	0.51
1953	Females	0.46	0.39
	Males	0.50	0.43
	Combined	0.51	0.41
1954	Females	0.45	0.44
	Males	0.43	0.37
	Combined	0.42	0.35
1955	Females	—	—
	Males	0.59	0.60
	Combined	0.47	0.40
All Years	Females	0.56	0.49
	Males	0.50	0.42
	Combined	0.55	0.43

[1] "Combined" sexes actually contains a number of fish that were unsexed, in addition to sexed fish.

Probability of dying for all ages combined:—The estimates of annual probability of survival, and its complement, annual probability of dying, were derived in two ways. A catch curve for males and females, and the sexes combined, shown in Fig. 18, was plotted on the semi-logarithmic scale, based on the data given in Table 15. An eye-fitted line was drawn and from this the survival rate was computed as the ratio of the numbers at two points on the line, spaced one year apart, the older divided by the younger. Another more formal approach consisted of computing these rates by the methods used by Ricker (1948:7–27) and Rounsefel and Everhart (1952:86–90), in which the lag differences of the age frequencies were weighted by the square root of the smaller frequency in each pair of comparisons to adjust for the small samples in the older age groups. By this method, weighted annual probabilities of survival and of dying were computed. Although a weighted death rate or instantaneous mortality rate was also computed, this statistic had no special pertinence in this study, hence it is left out. The unweighted and weighted probability of dying is summarized in Table 26 for the males and females and the sexes combined for the different years of collection. Unweighted values are used in the discussion, because they are used later in comparing mortality rates for fish from other studies.

Table 26 reveals that the annual probability of dying from 1948 to 1955 ranged from 0.38 to 0.59 for females, although most estimates were closer to the rate of 0.56 computed for the combined period 1948–1955. Among males, the annual probability of dying ranged from 0.37 to 0.59, but most of the estimates were close to the combined period, 1948–1955 estimate of 0.50. In general, males had a lower probability of dying than

females, a condition that is to be expected since females are larger and heavier, hence more vulnerable to the fishery. Thus, mortality is probably due largely to fishing rather than to biological or natural mortality. The former type of mortality can be considered a form of predation. The sexes combined resulted in a range of probability of dying of from 0.42 to 0.55, with most estimates close to 0.55 computed from all the data combined for the 8-year period. The probability of survival was also useful in gauging the average number of fish that survive from year to year from a cohort.

Probability of dying between various age groups:—An analysis of the empirical data for various age groups for all years combined indicates that the probability of dying is somewhat variable. Table 27 was constructed by taking the proportionate decrease between the two points on the right limb of the curve on the log plot, and calculating probabilities of survival and dying for age groups. When white perch reach the vulnerable, catchable age and size, between age groups V and VI there is a marked mortality, whereas between age groups VI and VII, mortality is somewhat less. Among the over-all calculated probabilities of survival for males and females, mortality decreases slightly between VII and VIII below the over-all probability of dying. After age group VIII, the probability of dying increased rapidly. A question as to which of these probabilities of dying most nearly describes the annual probability of dying for all age groups in the population as a whole is posed by Table 27. The first probability of dying for age groups IV–V seems to be influenced by age group IV which is not completely vulnerable to the gear used and so tends to reduce the slope at age group V. The second value at age groups V–VI in which occurs the greatest number of vulnerable fish probably more nearly approximates the true probability of dying based on all age groups combined, except that it may not apply to males that are smaller than females and hence are not entirely susceptible to the fishery. This can be seen by the good agreement that results when the estimates for specific age groups (Table 27) are compared with the unweighted probabilities of dying of all age groups of females and the sexes combined computed for all years in Table 26.

TABLE 27. Unweighted probability of dying calculated by taking the proportionate decrease between the two points of age groups of the right limb of the catch curve for male and female, and both sexes combined, of white perch, *Roccus americanus*, for the period 1948–1955.

Age group	Annual probability of dying		
	Females	Males	Sexes combined
IV–V	0.38	0.42	0.43
V–VI	0.54	0.57	0.57
VI–VII	0.49	0.59	0.53
VII–VIII	0.40	0.40	0.45
VIII–IX	0.77	0.83	0.79
IX–X	0.78	—	0.82

The variability among the males in these tables is very great. The probability of dying estimate of 0.57 for males between age groups V–VI more nearly approximates the estimated rate of about 0.63 determined by the regression line drawn for the plot of age frequencies for males in Fig. 18. The regression line estimates for females (0.56) and sexes combined (0.53) agrees well with the probability of survival estimates at age group V–VI and the computed unweighted probability of dying for all years. The values for the other age groups older than VI are variable, due principally to the smaller-sized samples, hence they are not subject to speculation. By the several avenues of analysis, it seems that annual probability of dying of females and the sexes combined are relatively low, and that the annual probability of survival seems to be relatively high for an exploited population.

Probability of dying among unexploited and exploited age groups:—There is some evidence that rates can be assigned to natural and fishing mortality among the younger and smaller fish, and older and larger fish, respectively. The first group of undersized fish are relatively unexploited by fishermen while the latter legal-sized fish are the exploited segment. The relatively non-selective sampling methods in shoal areas resulted in the capture of smaller, young fish that are not normally taken by netters and anglers because the legal minimum size is 8

inches. As far as could be determined these fish did not mingle with the larger fish. Assuming that this type of sampling caught smaller and younger fish that were spatially distributed differently than the larger and older fish, it is possible to determine the probability of survival and dying for this unexploited group. The data were examined for age frequencies of males and females taken largely by small-mesh gear in shoal habitats for the different years of collection. It was found that in certain years (1951, 1953, 1954, and 1955 for males; 1953 and 1955 for females) the use of experimental haul seines, bank dip nets, and small-mesh gill nets resulted in large numbers of younger fishes (see Table 15). The lack of older, larger fish from these collections indicated that differences in distribution were real. The probability of dying for males (1951, 1953, 1954, 1955) and females (1953 and 1955), although somewhat lower, agreed remarkably with the probability of dying obtained from older fish and for all ages and years combined. It should be stressed at this point that these estimates of "natural" mortality based on age frequencies among young fish are "apparent" probabilities of dying. In actuality, mortality may be brought about by emigration from shoal areas to deeper water as they become older and larger. Thus, they probably become unavailable and part of another differently-distributed population of older and larger white perch.

TABLE 28. Life table[1] for white perch, *Roccus americanus*, based on the known age at death of 3475 fish (both sexes combined), with a mean length of life 1.53 years.

x	x′	l_x	1,000 l_x	1,000 d_x	1,000 q_x	L_x	T_x	e_x
IV–V	−100	811	1,000	419	419	790	1527	1.53
V–VI	+228	471	581	331	570	416	737	1.27
VI–VII	+292	203	250	133	532	184	321	1.28
VII–VIII	+358	95	117	53	453	90	137	1.17
VIII–IX	+423	52	64	50	781	39	47	0.73
IX–X	+488	11	14	12	857	8	9	0.64
X–XI	+554	2	2	2	1,000	1	1	0.50

[1] Explanation of symbols used in table:

x is age in years = $\left(\frac{\text{Age}}{\text{Mean Length of Life}} - 1\right)$ (100%)

x′ is age as percentage deviation from mean longevity.

l_x is number of animals in actual sample of age group.

1,000 l_x is number alive (for each 1,000 born) at beginning of age group.

1,000 d_x is number dying (for each 1,000 born) within each age group.

1,000 q_x is probability of dying per 1,000 alive at beginning of age group.

$L_x = \frac{1{,}000\ l_x + (1{,}000\ l_x + 1)}{2}$ for each age group (x).

T_x = values of L_x summed from end of line for each age group.

$e_x = \frac{T_x}{1{,}000\ l_x}$ = mean length of life in years left for those at beginning of age group.

Life table for the white perch:—The life table is a concise statistical summary of certain vital statistics of a population. It has been applied to a wide variety of animals, among them, hydra, fruitflies, rotifers, birds, sheep, and man. If a sample of a group of animals consisting of members who start life together is complete and large enough, then the number of deaths, the remaining survivors, the rate of mortality, and the expectation of further life for each interval of age can be estimated under certain assumptions. The methods of tabulation and analysis were derived from Pearl and Miner (1935: 60–79), Deevey (1947:283–314) and Davis, et al (1956:52–61). The great value of life tables lies in their usefulness in seeking and understanding the forces underlying the crude, over-all population mortality. Since mortality varies greatly with age, especially among vertebrates, it is important to determine specific mortalities at as many different ages or life history stages as possible.

The age at death method was applied to the white perch data in collecting life table information. The starting point in the construction of the life table was the number of white perch in age group IV, many of which are sexually-mature adults. The data for the young fish below age group IV was not adequate for life table construction. With fishes, the starting point in the construction of a life table should be the number of fertilized ova or the number hatched, or the number of fish transforming from larvae to young fish, the raw data of which is virtually impossible to obtain in a natural population at this time.

The white perch life table (Table 28) consists of several columns, headed by standard notations, giving l_x—the number of fish out of a cohort of 1,000 fish that survive after regular time intervals of one year; d_x—the number dying during successive years in

terms of the initial population at the beginning of the period; and, e_x—the life expectancy at the end of each year. The mean life expectancy from age group IV for the cohort is slightly more than 1½ years. The values for other ages decrease after age group IV, and quite rapidly after age group VII. In general, the chances of survival among white perch at any one age is not very great. The causes of death below age group V would be due largely to "natural" or unknown causes, while above this age, mortality would be due largely to fishing effort or human interference.

Survivorship curves for white perch plotted from life table data, on the basis of logarithm of the number of survivors per 1,000 and per cent deviation from the mean length of life (under x' in Table 28) at each age, are very instructive. The relatively straight diagonal line indicates that the specific mortality rate beginning at age group IV at all ages is constant. This method of graphic representation can be used to compare species of widely different life spans. Such a comparison with examples given by Deevey (1947) shows that the white perch has a similar survivorship curve with the hydra, with at least six species of birds, and with survivorship curves based on synthetic life tables for snowshoe hare, pheasant and song sparrow.

Discussion

Interaction of Population Forces and Factors

General comments:—The interaction of the three forces—movements, reproduction, and mortality, theoretically combine to produce a typical white perch population at a given time and place. Although treated somewhat separately, these divisions are closely interrelated with one another. For an understanding of a population in an estuary it is necessary to look at it from different points of view by taking these forces into account. The magnitude of the primary forces is affected by changes brought about by important population factors such as environment, competition, and predation. The interrelationship of the general estuarine ecosystem, the three population forces, and the three environmental factors, in the light of the available data, is complex, but when synthesized, the degree of interaction is more clearly understood.

The environment of the white perch in the Patuxent River estuary is a changing dynamic medium (Pritchard, 1951:368–76), and it cannot be compared closely with an ideal constant environment where a population that is at equilibrium remains relatively stable. Fluctuations in numbers, growth, and population structure would therefore be expected in the white perch population. Theoretically, an ideal one would consist of individuals that are constantly changing, but whose number is relatively stationary. Assuming that it is in equilibrium with the physical habitat, where it has increased to the carrying capacity of the environment, the changing elements of the population will be those fish that are reproducing, growing, and dying, and natality will be balanced by mortality. After a white perch spawns, the number of eggs emitted and larvae hatched will be greater than deaths, but at capacity the recruits ideally should equal deaths. It can be hypothesized that when the population is below capacity it will increase to this level along a sigmoid growth curve. The increase at first is slow, then rapid and then slow again, until at equilibrium it diminishes to zero. Within the Patuxent River estuary environmental factors fluctuate greatly, and certain biological aspects either fluctuate directly or inversely with these environmental factors. Such density-independent aspects, on the one hand, while rarely favoring stability, would tend to bring about variations, sometimes drastic, in population density, causing a shifting of carrying-capacity levels. Density-dependent aspects, on the other hand, such as natality and mortality, would tend to maintain the population in a "steady-state" or to hasten the return to such a level. The actual effects would be to bring about fluctuations in population level because of the varying combinations of density-independent and density-dependent factors. The data indicates that some of the total effects can be measured, but a breakdown of the factors is a highly complex task.

One of the ways to gauge the effects of reproduction and mortality in a population is to determine the existence and nature of year-class fluctuations. White perch lend themselves nicely to this type of analysis since in any one year collections involving up to 9 year-classes can be sampled. Thus, any study involving annual changes in population density, reproduction and mortality must be preceded by an age and growth study. Evidence was introduced to show that the results can be biased by sampling, gear selectivity and errors of measurement. If great care is not exercised in processing and aging scale samples, this bias can greatly affect the estimates of mortality and certain aspects of reproduction. The back-calculating method of estimating previous lengths at each age was utilized in determining the growth history of year classes from 1942 to 1956, as well as for a general curve of absolute growth. Observations made on the length attained by each age showed good agreement between the observed and calculated lengths.

Gear selectivity greatly affects the vital statistics of white perch in the Patuxent River. It is probable that the selective action of the large-meshed fish-nets serves as the basis for differential destruction, associated with growth rate, that brings about an exaggeration of the discrepancies at early ages between calculated growth rates of white perch. It follows in an intensive fishery, with a high minimum legal size of 8 inches, that a severe mortality of the faster-growing fish of the younger age groups is certain to occur. This apparently happened in the Patuxent since great differences were found between mean sizes at corresponding ages of fish taken by various gear. Also, certain large fish in age groups III and IV, the mean sizes of which will not normally enter the commercial fishery for several years, were found to be susceptible to capture. This is a probable explanation of why white perch of the same year-class captured at older ages show relatively slow growth not only because the samples of the younger age groups were composed of the faster-growing fish, but also because some of these same fast growers were eliminated from the stock as young fish.

Differential probability of dying connected with the rate of growth that decreases with the attainment of greater age in poikilothermic animals was found to occur among white perch. The detection of this fact, however, is greatly complicated by the effects of fishing intensity by the various methods cited above; thus, it is not possible to make precise estimates of the extent to which reliability of the samples of the different age groups was affected by the selective action of the gear. Of those fish taken by commercial gear, it is obvious that fish in age group I demonstrated the most rapid growth. This factor is probably an important explanation of differences in the observed and calculated growth rates for the early age groups for both sexes. Beyond age group III, gear selection probably had no significant effect on the reliability of the samples for growth estimates.

Age and growth:—Age and growth studies are necessary for understanding the vital statistics of white perch. Age analysis of females and examination of the gonads in different stages of development, for example, indicated the time and size of attainment of sexual maturity. Thus, males matured earlier than females; this fact was a partial explanation for the unequal sex ratio as reflected by the preponderance of males observed on the spawning grounds of white perch. The age at which both sexes enter the commercial and sport fishery was of great value in elucidating certain relationships between growth and population density given below. Many factors affect growth rate, among them—temperature, food supply, and in certain cases, population density. The most impressive effect of temperature on the growth of white perch can be seen on their scales, which allowed estimates of age and growth rates. During winter, the cessation of growth is reflected in the form of "winter rings" or annuli between the circuli laid down one year and beginning the next. Although data was collected on food habits, the lack of quantitative data on available food supply in relation to feeding and rate of growth did not allow any speculations on this point.

Comparisons of rates of fish growth be-

tween bodies of water may partly identify good and bad environmental conditions. Also, comparisons of longevity and growth are a crude measure of the effects of reproduction and mortality, which in turn are influenced by environment, competition, and predation (including man). A comparison of the growth rate of Patuxent River white perch with those from other localities is plotted in Fig. 19. Except for Saila and Horton (1957:30) none of these studies have employed a scale-length and body-length correction to back calculation of growth at the various ages. Some are based on average sizes of observed age groups. For this reason, these growth rates are not quite comparable, especially at the early ages. The crude graphic comparison, nevertheless, reveals some interesting geographic differences in growth. Some, it must be admitted, are more apparent than real.

The Maryland growth curve overlaps reasonably well with the two growth curves for Maine given by Cooper, and Fuller and Cooper. Rupp (1954:49) and AuClair (1956:26) generally corroborated these comparisons for Maine fish. The major difference between the two regions is that very old fish were observed in Maine, some reaching 16 years of age. The average life span of Maine white perch is about 7 years, while it is about 4 years in Maryland. No fish older than 10 years was recorded from Maryland waters, and none over 6 years old were recorded in North Carolina. Growth rates for white perch from states other than Maine were found to differ widely from the Patuxent River growth curve. North Carolina white perch attained the same size at age VI as Patuxent River fish at age X. Since some of the studies are known to be based on small samples and possibly on methods of collection that were selective for either fast-growing (as in Massachusetts) or slow-growing (as in Nova Scotia) fish, it is obvious that most of these differences are of no important significance. Cooper took large samples by various gear, some selective for large size and others non-selective, so that his data are the most complete and comparable with Patuxent white perch.

These points emphasize the fact that

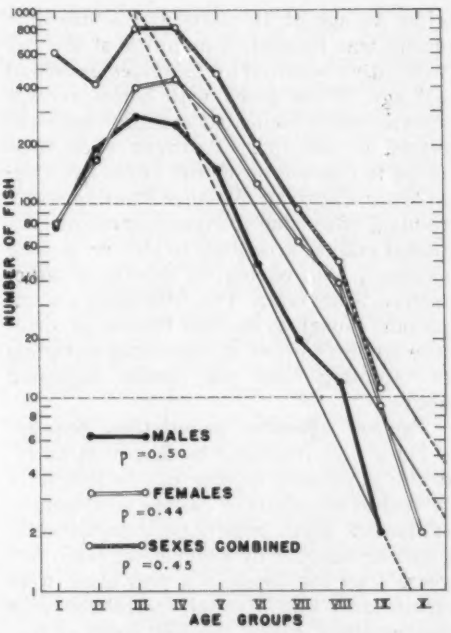

Fig. 18.—Catch curves for white perch, *Roccus americanus*, based on the combined collections from 1948 to 1955, Patuxent River, Maryland. Regression lines have been fitted by least squares method to provide probability of survival (p).

growth rates of fish from different areas can be compared when identical methods of sampling are utilized. A primary factor to consider in comparing growth rates of fish from different geographic regions is the magnitude of the productive capacities of the waters they inhabit. The white perch tends to become very abundant and dwarfed in many lakes which Cooper (1941:122) has attributed to limitations of food supply. Stroud (1955:21) and Saila and Horton (1957:30) did not find stunting to be the usual condition in their particular surveys, but they did emphasize the low rate of angler utilization, even when white perch showed relatively good growth. Cooper found that growth was so slow in some lakes that it required from 6 to 10 years for most fish to reach a length of 6 to 8 inches. In other lakes the white perch had grown to a length of over 9 inches in 6 to 8 years or less. Cooper concluded that

after an age of 10 years and a size of 8 inches was reached, a majority of the fish were either removed by fishermen or died of old age. White perch with below average growth which indicated stunting were observed in the upper Patuxent when compared to faster-growing fish at the same age in lower Patuxent. Whether stunting was a residual effect due to consequences of continued culling according to size or to food shortage, high population density or other factors, is unknown. The differences are important enough to warrant the design of future studies toward a better understanding of "stunting" and the factors suggested above.

Factors affecting population density: —Data were presented to show that an index of population density can be indirectly related to the effects of various environmental factors. Thus, large populations of white perch as reflected by commercial catch five years after the hatch of a year class, were significantly and inversely correlated with size attained during the first year of life. Large numbers of fish in the commercial catch were related to white perch that averaged small sizes; small numbers of fish in the catch were related to fish that averaged large sizes. The first-year growth, in turn, was negatively correlated with rainfall in spring, positively correlated with growing season in spring, and positively correlated with solar light energy. These relationships, therefore, can be shown to have their effect on the success of reproduction. The association between reproduction and environment, with a resultant mortality depending on the interaction, gives a firm foundation for predicting the effects on one, given the data for the other.

The remarkable relationship between first-year growth of white perch and the index of population density has precedency in several other studies with fish populations. Differences in growth rate of an animal population related to its abundance must be studied from a long-term standpoint in order to gain a true perspective of the relationship. Davidson and Vaughan (1941:243-4) concluded, after a study of the pink salmon fishery in southeastern Alaska from 1895 to 1940, that when populations are large in numbers the individuals composing them are usually small-sized. On the other hand, when the populations are small in number, the individuals composing them are usually large-sized. Foerster (1944:279) also found a statistically significant inverse correlation between the population size of sockeye salmon in Cultus Lake, British Columbia, and the size of the migrant fish. He concluded, generally, that the body size of migrant salmon is affected to a certain extent by the density of the lake population.

Data on limiting factors of white perch populations is not available, but the results of certain aspects of this study suggest that since the growth of this species is negatively correlated with numbers, food supply may be a primary limiting factor. Thus, white perch with small first-year growth are related to large populations which are subject to a high intraspecific competition for the available food. The corollary also apparently exists, i.e., fish with relatively large first-year growth are related to small population densities that have apparently taken fuller advantage of the food supply. Food is a density-dependent factor, and it is profoundly affected by the broad density-independent variations in the physico-chemical nature of the aquatic habitat. Food for larvae and juveniles consists either of other aquatic animals or plants which have been shown to be dependent entirely upon certain essential elements dissolved in, or, in the case of sunlight, acting through, estuarine water (Tait, 1952:81–8). Rainfall, water temperature, salinity and solar radiation either directly or indirectly affect the availability of the essential constituents necessary for survival of young stages during and after spawning. The nutrient salts, nitrates and phosphates, especially the latter, have been shown to be those most likely, according to Liebig's Law of the Minimum, to limit phytoplanktonic growth in the sea, by their presence only in the minutest traces, or, by their complete absence, to stop it altogether. The Law of the Minimum can be applied further to white perch, i.e., not only must sufficient food be

available, but all those other factors which in any way promote the growth and development of white perch must exist in sufficient amount to act in conjunction with food.

Movements and subpopulations:— Among the population forces, movement can often bring about pronounced change in activity and numbers of white perch. Fish in marine and estuarine waters undertake seasonal movements either for spawning, feeding or over-wintering. The tagging investigation indicated that the Patuxent River white perch was an isolated and self-contained population, although within the Patuxent estuary it undertook large-scale migrations for spawning from brackish to fresh water. The rate of recapture (10.7%), indicating a poorly-exploited species, is considered adequate to show the major features of seasonal movement. Stroud (1953:274) and Stroud and Bitzer (1955: 56–7) are the only investigators who have tagged white perch. Their returns were very low (N = 270 tagged; N = 3 recaptured, or 1%) in areas where effort for the species was low. There was virtually no interchange of Patuxent white perch with those from Chesapeake Bay or tributaries. A physiological basis for movement from salt to fresh water has been given by Hoar (1952: 437–52); in general, some movements are forced for physiological reasons. Salinity is considered an effective barrier against emigration.

The white perch might be classified as semi-anadromous on the basis of its movements. Although estuarine populations are restricted in brackish areas during the year, except for spring, their generally euryhaline nature does not fully restrict them there. Movements would tend to decrease or increase the numbers of a population but in the Patuxent River this condition did not occur except locally and seasonally. Tagging studies and collections of spawning-ripe fish caught by commercial fishermen, in addition to collection of eggs and larvae in plankton nets, have delineated the spawning area in tidal fresh and slightly brackish water in the upper Patuxent.

Migrating schools of white perch during spring months become vulnerable to human predation along most of the estuary, whereas at other seasons they are subject to more restricted fishing. Angling, while intensive, probably takes only a small part of the total catch. Slightly less than 8% of all tag recaptures were made by hook and line (Table 6). Large segments of the adult population move from one section of the river to another for a period of several weeks to two months. In a sense, all three forces—movements, reproduction, and mortality, are in operation, more or less affected by the primary population factors. After spawning they return downstream to the brackish areas in the mid- and lower estuary. White perch tagged in summer did not exhibit long-range upstream or downstream movements. Their activities and limited movements are believed to be associated with greater food supply in the area from Zone III to V. Nash (1947:170) stated, for example, that freshwater plankton from the upper estuary and saltwater plankton entering the lower Patuxent estuary from Chesapeake Bay generally reached the mid-estuary. The combined effects of the two great sources of food are believed indirectly to contribute to a greater food supply. Movements of white perch tagged in autumn were not clearly defined, but in general after water temperatures began to lower, most returns came from deep water downstream from the tagging site. During the winter months all returns came from water ranging from 20 to 100 feet deep in the mid- and lower Patuxent. Those fish tagged from very deep water in winter were active and feeding. Generally, it can be concluded that in the Patuxent River, movements are necessary for the forces of reproduction and mortality to operate.

Of the few fish that left the Patuxent River, the direction of their movements suggested that they could have entered the Potomac and Nanticoke Rivers, respectively. The possible relationship between the white perch from the three estuaries was investigated. The means of the character index of the Patuxent River fish were statistically different ($p = <0.01$) from that of Nanticoke River, but not from

the Potomac River fish. A *t*-test of the significance of the difference of the means between the Patuxent and Potomac Rivers indicated there is no evidence that they came from populations that are different. Woolcott (1955:70–2) also presented evidence to suggest that the two tributary populations were not significantly different. Probably the only explanation for the similar mean character indices of white perch between these estuaries is, in spite of the apparent lack of interbreeding, that they were populated by the same post-Pleistocene migrants. Environmental conditions in the two rivers perhaps vary in the same way from year to year. Raney and de Sylva (1953:505) did not obtain significant differences between the mean character indices of striped bass from the Potomac and Patuxent Rivers. The sample means for the character indices shown in Fig. 17 do not follow a geographic trend or cline of low value in the south to high values in the north as might be expected. Raney and de Sylva (1953) and Raney (1957:106–7) also were not able to show a cline of the character indices of striped bass for various populations sampled in Chesapeake Bay. Woolcott (1955:53) stated that within Chesapeake Bay most structural details such as body and head depth and pectoral fin length, showed a clinal tendency to increase southward, often reaching the maximum at the Rappahannock or York Rivers. Woolcott (1956:414) concluded from his study of the infraspecific variation of white perch throughout its range that there were two primary gene pools located north and south of the Delaware River. His results (1955:46, 55) generally corroborated the present study of Chesapeake Bay subpopulations, in that the fin-ray counts for the James River population is considerably lower than those from upper bay samples. He also found that the fin-ray counts were generally higher in the Hudson River and lower in Chesapeake Bay tributaries, whereas in the striped bass, which occurs sympatrically over a part of the range, the reverse is true. He suggested that this difference lends support to the belief that many differences between populations within each species may be genetic rather than due to environmental influence.

Meristic studies have posed some important questions regarding movements, reproduction, and environment. Meristic characters and their numbers in local populations are genetically fixed within narrow limits. Schmidt (1917:279–397) has shown that some fine "racial" distinctions are inherited. A growing body of evidence has been presented by Rounsefell and Dahlgren (1932:270–3) and others to show that minor fluctuations that occur in meristic numbers from year to year within a population are believed to be due to different physical and perhaps chemical conditions at any one locality or differences in time of spawning. Such fluctuations will tend to balance out when samples are taken over a period of several years from the same locality. The effects of environment, therefore, cannot be neglected. Rounsefell and Dahlgren, for example, showed that the means of the vertebral count for nine successive year-classes for the Pacific herring were negatively correlated, $r = -0.85$, with temperatures during the spring months when spawning and incubation occurred. The results of the meristic and tagging study of white perch have shed no light on the degree of intermingling of Chesapeake Bay subpopulations, especially between closely associated ones. Further corroboration of the existence of subpopulations in all major tributaries and different areas of the bay is urgently needed, with direct confirmation by tagging. These phases should be followed up by experiments to clarify the genetic and environmental implications of subpopulations.

Reproduction:—Natality is the inherent ability of a population to increase its numbers. Ecological natality, which is the population increase under actual environmental conditions, can be roughly surmized from year-class fluctuations and from the relationship of first-year growth and the index of population density discussed above. These data would indicate that ecological natality is not a constant for the population but may vary with certain physical environmental conditions and possibly

with the size and composition of the population. A full understanding of the force of reproduction in white perch cannot be comprehended at this time in the absence of data on fecundity, egg and larval production, and survival at different early stages of development and under different environmental conditions. This study has been instrumental, however, in suggesting important methods of sampling and techniques in collection that will provide estimates of these aspects of reproduction in future studies.

Reproductive data are presented to show various estimates of the age and sizes at spawning of the sexes, with details on the time, duration, and location of spawning. These results are similar to some presented by AuClair (1956:19–20). The white perch produces huge numbers of eggs per individual—50,000 to 150,000 eggs. After ovulating at random, the females leave their eggs to survive as best they may with no parental care. A general principle that has been developed empirically by fishery scientists is that in fishes with large numbers of eggs, survival and fluctuations in abundance are due more to the environment than to the actual number of eggs deposited or the size of the adult stock. Thus, to obtain good survival, and hence good recruitment to a population, there apparently has to be an optimal combination of certain factors such as temperature, rainfall, salinity, solar radiation, and other environmental factors for optimum spawning. Thus, if the principle applies to the white perch, then there is an association between these environmental features and the results of reproduction and subsequent population densities.

Although the data indicates that white perch spawn but once a season, the occurrence of a large proportion of fish with partly spent gonads indicated that a single individual does not expel its full complement of eggs at one time. The various degrees of the partly-spent condition indicated that eggs might be expelled on more than two or three occasions probably depending on biological and environmental stimuli. Water temperatures fluctuated markedly during the spawning season, and since this factor appears to exert an important influence in determining time of spawning, it may be of primary concern in rate of spawning for 1953. It is conceivable that fluctuating temperature and other hydrographic factors can shift the time of spawning at least a week in either direction from year to year. Observations made on the spawning grounds at Queen Annes Bridge and near Nottingham on the Patuxent River during 1954 and 1955 indicated that the peak of spawning was about the same as in 1953. During 1956, however, it occurred more than a week later than that recorded for 1953.

Data on the spawning of Patuxent River white perch agrees well with most published observations. Smith (1907:275) stated that the spawning season (April 1 to 10) is short in the Albemarle, North Carolina region, whereas Hildebrand and Schroeder (1928: 244–7) found that the spawning season at the head of Chesapeake Bay reaches its height in late April and early May. The latter authors found that males outnumbered the females on the spawning grounds by 3 to 1. Also, an important exception is made to part of their observations. Their conclusion, based on "10 ripe males and 3 ripe females" taken in early December, 1915 in Chesapeake Bay, that spawning may occur in winter under certain conditions, is erroneous. Bigelow and Schroeder (1953: 405–6) apparently accepted the observation without offering further evidence. This extraordinary observation is true for males in the Patuxent and elsewhere (Saila and Horton, 1957:30) in the sense that they are in spawning ripe condition, but it is not believed to be reliable for females. Since virtually all females taken during winter by Hildebrand and Schroeder were caught by trawl in deep water which may subject the fish to being packed and crushed in the cod-end of the net, it is plausible that ova from the "3 ripe females" were observed extruded under great pressure. Female white perch with extruded ova were also observed during the present study in the catches of drift gillnet fishermen in January and February; the extrusion was due entirely to pressure forcing the unripe eggs through the urogenital

pore. A large number of adult females with well-developed, enlarged ovaries were examined from winter collections from the Patuxent River fish, but none was observed in spawning-ripe condition. The evidence from the present study, therefore, does not support the premise that spawning may occur in winter.

The predominance of males on the spawning grounds and of females in the lower estuary during the same time in April and May was marked. An unequal sex ratio has been noticed for other species of fish. Merriman (1941:19) observed predominantly males of striped bass at spawning time and stated that 10 to 50 small males may accompany a single female weighing 4 to 50 pounds. Eschmeyer (1948:35) stated that the walleye pikeperch on the spawning grounds consisted of 89 per cent males. This species has a remarkably similar spawning pattern to the white perch. Female walleyes attained their maximum numbers (28 per cent of the catch) near the peak of the spawning season. Among white perch, females attained their maximum numbers (35 per cent of the catch) near the peak of the season. A single observation on the courtship behavior of white perch indicated that many small males attend one or several females much in the same manner as described for the striped bass. There is no simple, clear explanation for the unbalanced sex ratio, although the further study may show that it is related to age and size at sexual maturity, differences in spawning migrations, different behavior between the two sexes, and possibly to selective fishing. The problem is further complicated by the predominance of females in the samples in the lower estuary throughout the spawning period, even though tagging evidence showed that virtually all recaptures from this group were taken upstream on the average of 11 miles (with upper extremes of 34 miles) from the site of tagging.

The age and size at maturity is of considerable biological significance, since males mature earlier and at a somewhat smaller size than females. Radcliffe and Welsh (1917:42) discovered examples of both sexes 125 and 170 mm in length (probably T.L.), averaging 0.11 pounds in weight, in spawning condition, while the smallest ripe fish recorded by Hildebrand and Schroeder (1928:246) were: male—109 mm; and female—121 mm. All males of age group II, whose numbers in the populations are proportionately greater than older age groups, as well as these older fish, invade the Patuxent spawning grounds. These very small fish account for the unbalanced sex ratio in this river and on the spawning areas throughout its range. Very few age group II and only a portion of age group III females are sexually mature, hence in any samples where an equal sex ratio would be expected on the spawning grounds, it is obvious that the lack of the non-migratory immature fish in these age groups would result in predominantly males. Males in age group II comprised 80 per cent of all the fish tagged on the spawning grounds. If these are subtracted, the percentage of males is reduced to 64 per cent. If the loss for II and III year old immature females to spawning could be compensated, then an equal sex ratio might be approached. Selective net fishing undoubtedly removes proportionately more larger-sized females than males on their way upstream to breed.

The age and size at maturity also has an important bearing on the management of the white perch, which in turn affects the biology of the species. Marked differences were recorded between the mean sizes and ages of the two sexes from samples studied at the same time in Zone I and V. Generally, larger older fish were sampled downstream, the opposite upstream. These differences may have represented two populations, or the smaller, younger fish could have represented a heavily fished population whose phenotypically large fish were systematically removed by heavy fishing pressure in spring. As has been shown, the minimum legal-sized mesh in almost all gear is selective for size, thus the larger young and larger old fish are selectively culled by the fishery. It is conceivable that if fishing intensity is sufficiently high, the remaining smaller fish, if they are genotypes for smaller fish, will produce future crops of

smaller fish. This thesis of phenotypical selection, of course, is in general conflict with the modern genetic type of selection and the importance of recombination of genes which does not place emphasis on the external features. Present information emphasizes environmental influences over genetic factors; overcrowding produces stunting in growth, undercrowding or sparse populations demonstrate greater than average growth. If it can be demonstrated by laboratory rearing of white perch that progeny selection is taking place, then such selective fishing can have serious effects on the future sizes and age distribution in the population.

Mortality:—Mortality of white perch in the population is usually expressed as the number of individuals dying in a given period. Ecological mortality, which is the loss of individuals under a given environmental condition, is not a constant but varies with population and environmental conditions. The theoretical minimum mortality, which would represent the loss under ideal or nonlimiting conditions, probably is not in operation in a changing dynamic estuary. Under these ideal conditions white perch would die of "old age" determined by their physiological longevity. Population fluctuations, as indicated by the first-year growth and commercial catch inverse correlation for 9 consecutive years, suggests small but differential mortality. Thus the first-year growth fluctuations are believed to reflect natural mortality resulting from density-independent environmental factors and population density.

Longevity of white perch varies along its geographical range. Earlier, when growth rates of white perch from different states were compared, maximum ages for the different regions were indicated (Fig. 19). The highest was recorded in Maine, where some white perch reached the age of 16 years. Those from other New England and Middle Atlantic States attained 10 or less years of age, while a single study in North Carolina revealed a maximum of 6 years of age for the sample. The study in Nova Scotia is at variance with the general trend from north to south of declining maximum duration of life, probably because of an inadequate sample. The relationship between maximum ages attained and length of growing season from north to south suggests the generalization developed by Pearl (1938:482) that: "the length of life is generally in inverse proportion to the rate of living." Thus the more rapid the pace of living is, as in the case of organisms living in waters with higher average temperatures and longer growing seasons, the shorter the time that life endures. The duration of life of an individual white perch is the net resultant of the interplay between its own innate biological makeup and the forces acting upon it, favorable or unfavorable, external and internal. In the case of white perch populations that are unexploited or exploited by human predation, an important distinction can be made between changing the maximum and average duration of life. The span of white perch cannot be lengthened in any one ecological area by restricting fishing since each population has its own span of life influenced by environment and heredity. Restrictive fishing, however, can alter the average duration of life. Because more of them escape nets and other forms of human predation through size regulations, absolutely more of them survive at later ages but at smaller sizes.

Data on mortality indicates that white perch are apparently not being overfished in the Patuxent River. The annual probability of dying, on the average, is not much more than 50 per cent of the population at any age after age group IV is attained. Females, which grew larger and heavier, especially in spring as a result of the force of reproduction enlarging the gonads, are more susceptible to capture than males. In spite of this type of selection, the former attained an older age. As shown in Table 11, the mean age in years for all females (3.97) was greater than that of males (3.49), and the differences were statistically significant. Here again, the subject of bias is introduced by the selection by gear of larger and presumably older fish, although the data established the fact that females reach significantly larger sizes at corresponding ages. It is presumed that gear se-

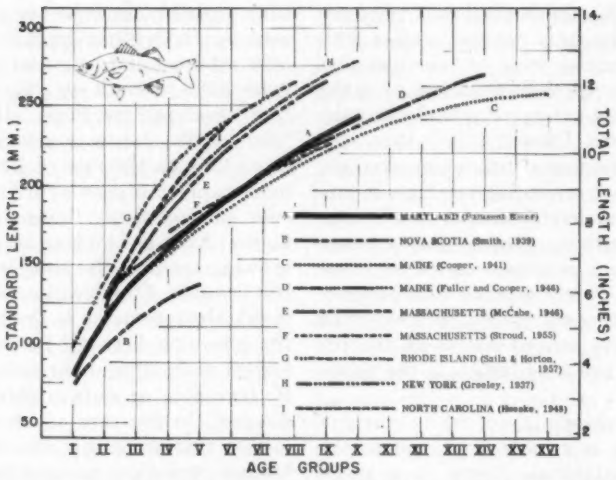
STANDARD LENGTH (MM.)
TOTAL LENGTH (INCHES)
AGE GROUPS
I II III IV V VI VII VIII IX X XI XII XIII XIV XV XVI
A MARYLAND (Patuxent River)
B NOVA SCOTIA (Smith, 1939)
C MAINE (Cooper, 1941)
D MAINE (Fuller and Cooper, 1946)
E MASSACHUSETTS (McCabe, 1946)
F MASSACHUSETTS (Stroud, 1955)
G RHODE ISLAND (Saila & Horton, 1957)
H NEW YORK (Greeley, 1937)
I NORTH CAROLINA (Hooke, 1948)

Fig. 19.—Gross comparison of growth curves of white perch, *Roccus americanus*, from the Patuxent River, Maryland, with those determined by out-of-state studies.

lection may have been an important factor in defining the difference in the mean age at capture of the two sexes by all methods of collection.

There are no published studies dealing with annual probability of dying derived from age frequencies of white perch from other areas with which to compare the Patuxent River data. The age study by Cooper of white perch taken from various lakes and ponds in Maine in 1938 and 1940 provides some raw data for gross comparisons of the rate with the Maryland data. Although Cooper's fish were distributed in a number of freshwater impoundments, his samples are large enough among the older groups for the construction of an artificial catch curve for his entire sample. Fig 20 shows that when the Maine catch curve is compared with the Maryland catch curve, there is an interesting similarity in the right limbs. An obvious difference is the marked shift on the age scale to the right for Maine white perch. The computed probabilities of survival and dying ($p = 0.48$ unweighted; 0.60 weighted; $q = 0.52$ (uw); 0.60 (w)) for this sample of white perch from Maine are similar to Patuxent River fish. The somewhat higher probability of survival of Maine fish may indicate that the exclusive sport fishery is not able to exploit the stocks as do the commercial and sport fishery combined in the Patuxent River.

Studies of the mortality rates of other species of fish generally agree with the white perch data. That is, the probability of dying generally increases with age above age group IV. Among other species of fish, Ricker (1947:114–28) has shown that in a number of unexploited populations mortality rates increased steadily with age over the range in which it could be measured. Among whitefish of Shakespeare Island Lake in Lake Nipigon, the probability of dying was very low, varying from 8 per cent at age group XII to 17 per cent at XX, and up to 45 per cent at XXVII. Among whitefish of Lake Opeongo, on the other hand, the probability of dying was much higher, even without fishing, varying from 41 per cent for age group VII to 59 per cent at XIII. Since some of the whitefish live as long as 26 years, these differences are quite remarkable for the two groups of fish in Ontario, Canada. The unexploited populations of rock bass studied by Hile indicated that the oldest fish died off rapidly.

Observations indicate that the probability of dying among young unexploited age groups of white perch is slightly less than

that of older exploited age groups of white perch. If this is generally true among small white perch, then the computed annual probability of dying can be extrapolated to younger age groups with greater confidence. There is reason to believe, as pointed out earlier, that "mortality" among small young fish may be due to emigration from shoal to deep water areas, where they mingle with larger older fish. The most interesting suggestion from these data, if there is "real" mortality among young fish less than age group V, is that when they are below legal size, the natural mortality roughly equals natural mortality plus fishing mortality of the older fish. This suggests that the rate of natural mortality becomes much less once exploitation begins. Miller (1949:180–6) compared the catch curves of ciscos from unexploited and exploited lakes in Alberta, Canada, and found that the annual probability of dying in an unfished lake may exceed the probability of dying in a lightly fished lake. He suggested that natural mortality rate is influenced by fishing mortality rate, and from the white perch data it may be inferred that fishing mortality decreases natural mortality.

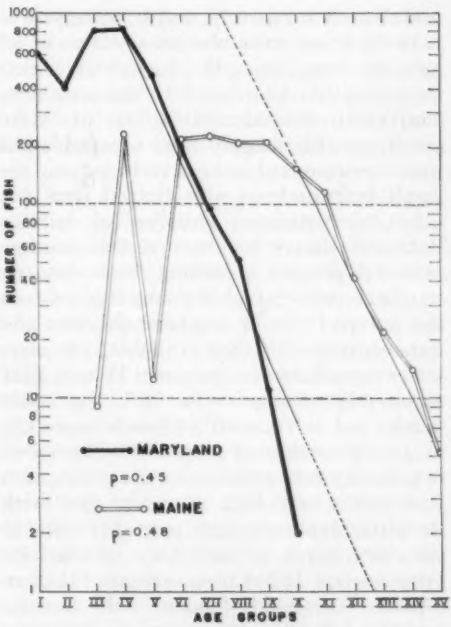

Fig. 20.—Comparison of catch curves of white perch, *Roccus americanus*, (both sexes combined) for Maryland and Maine.

Life table:—A detailed life table has never been tabulated for fish population, although the life table method has been applied to a number of aquatic invertebrates and higher vertebrates. Pearl and Miner (1935:69) pointed out that although enormous numbers of eggs and larvae produced by certain teleost fishes are subject to an extremely heavy mortality at the beginning of life, the relatively few survivors must be regarded as biologically differentiated from those eliminated. The latter have the power to go on living, with only a comparatively slight mortality, to the completion of a relatively long span of life. Deevey (1947:229–301) has lucidly discussed the reasons and difficulties in constructing a life table although the problem of aging in fishes is minimal since scale analysis is one of the most reliable dating tools among animal populations. Life tables for fishes, according to Deevey, are difficult to construct for these reasons: (a) fishes of all ages cannot be caught with equal facility; (b) they exhibit variable annual recruitment; (c) reliable data on relative numbers of very young and very old examples in the population are generally lacking; (d) mortality rates change with age; and (e) mortality between egg stage and metamorphosis from larvae to young is all out of proportion to mortality above age group I.

The objections given by Deevey are generally valid, but they apply more or less to all groups of animals, especially those species having very high fecundity rates coupled with very high mortality rates early in the development. The need to investigate the applications of a life table among species of fish for which some of the basic conditions are fairly well-satisfied is very great. For this reason, a life table for the white perch was constructed, with reservations, in an attempt to understand more fully, age-specific mortality rates. The white perch data shows the following relationship to Deevey's objections: (a) size and age selection by gear has been studied

and treated extensively, and an attempt was made to offset unequal representation of all ages by sampling with non-selective gear for younger and smaller fish; (b) some fluctuation in annual availability of white perch, resulting largely from a variable annual recruitment has been recorded, but its small magnitude is such that it does not affect the estimates greatly; (c) reliable data on relative numbers of fish younger than age group I is lacking; some data on numbers and survival of young fish between age groups I and IV has been obtained and data on very old fish is available; (d) mortality rates between age group IV and VIII apparently change very little in white perch; and (e) mortality rates between egg stage and postlarval stages in white perch is probably very great, since the white perch possesses a very high fecundity rate, with its attendant very high mortality rate in the early stages, as have been recorded for other species. It has been estimated that an 8-inch, 5-year-old female, will produce roughly 150,000 eggs during a spawning period. The latter factor is the reason for not setting the origin of the life table at hatching.

The mean life expectancy of 1½ years for the white perch extracted from the life table is low when compared with the Dall mountain sheep, herring gull and lapwing, as shown by Deevey. On the other hand, it compares favorably with the relatively low mean life expectancies for the blackbird, songthrush, robin, and starling, all of which have the same general life span as the white perch. The survivorship curve for adult white perch differs from civilized man, Dall sheep, rotifers and possibly the barnacle in that the curve for the latter group of organisms is convex, indicating that the mean life span is stretched toward the maximum. At the other extreme, the concave, or J-shaped survivorship curve is characteristic of oysters, and as implied above, among fish with very high reproductive and low survival rates in the egg and larval stages. If more data were available among the early developmental stages of white perch, undoubtedly the survivorship curve would be of this type. There is an obvious fallacy in comparing widely divergent animal forms by this method when it is known that the life table begins at different biological ages. This is true among accepted applications of the life tables to different phyla of animals, and it is especially true with the white perch, where detailed facts about numbers and mortality of the youngest ages are not fully available. Rearing white perch under controlled laboratory and field conditions may provide an insight into this problem. Until further evidence is available to corroborate the calculations given above for the white perch, it is best to consider this life table provisional and applicable only to adult fish.

The relationship of the white perch to its environment is subject to complicated factors in its ecosystem. The populations exhibit some fluctuations in abundance, in vital statistics, and variations in age and size. Statistics and estimates are presented for some of the population forces and factors with sufficient precision so that the magnitude of certain fluctuations and changes can be predicted. Data on reproduction at the primary level of fecundity, numbers of fish spawning, numbers of eggs and larvae surviving, and other aspects, are needed to corroborate estimates of recruitment obtained by indirect methods. Knowledge of mortality at the primary level is also lacking. The probability of dying estimated from age frequencies for adult fish indicates that the rates are generally stable. Thus, in spite of observable but apparently small fluctuations in first-year growth with population density for at least 8 year classes of white perch, the population appears to be generally stable. Further details are required on the population, environment, competition and human predation. A detailed investigation of the extremely important subject of interspecific competition was not possible during this project, but Cooper (1939:58–60), and comments on his work on white perch by Rounsefell and Everhart (1953:353–4), suggested a beginning to a complex problem. The habitat and its carrying capacity is fundamental in the determination of the size of the population, although there are indications that competi-

tion may also exercise an important influence on numbers. Natural predation, parasitism, and interspecific, as well as further details on, intraspecific competition, in open river systems and landlocked conditions, deserve increased attention throughout the geographical range of the species.

Management Implications

Five aspects of this study are pertinent to the management of the white perch in the Patuxent estuary: (1) the species is self-contained in the system despite its ability to leave the river, hence it can be managed on a local basis; (2) it has a high reproductive potential and is able to spawn several times (males for 3 or 4 seasons and females at least 2 seasons) before being legally vulnerable to angling and netting at 8 inches total length; (3) the average rate of growth for both sexes in the Patuxent appears somewhat below the mid-area of the crude National growth curve based on studies from Nova Scotia to North Carolina; (4) the average sizes and ages of both sexes of the Patuxent population are low and less than the 8-inch, age group V, minimum category for legal-sized fish, primarily because regulations and fishing gear promote the removal of larger, faster-growing fish, and further, the age frequency distribution of sizes indicates that at any one time only about one third of the entire population may be available as keeping-size fish; and (5) the numbers of the population are not being overfished, since the probability of dying of older fish, which reflects exploitation, is not high.

The points above suggest the following considerations for management of the species in the estuary: (1) specific regulations can be put into effect for the Patuxent on a controlled management basis without affecting stocks elsewhere; (2) size limits can be reduced or removed entirely without seriously affecting reproduction, since prodigious numbers of both sexes of white perch begin spawning at a small enough size to avoid exploitation or to discourage fishermen; (3) reduction or removal of size limits will thin down and reduce overcrowding among the great numbers of unexploited fish between 5 and 8 inches total length, reduce the exclusive exploitation of fish 8 inches and over, step up the rate of growth, perhaps increase the average length of individuals in the population, and possibly improve their catchability; (4) the probability of dying among the unexploited, sub-legal fish, which is somewhat similar to that of the exploited, legal-sized fish, suggests that unless a part of the sub-legal fish are utilized by fishermen, they will be lost to natural causes no matter how managed; (5) while spawning area and habitat improvement, other types of environmental control, and reduction of unusual competitors adapted to estuarine conditions as is the carp, *Cyprinus carpio,* are not clearly indicated at this time, constant vigilance is required for optimal maintenance of the spawning areas and estuarine habitat, and the effects of deforestation, runoff, siltation, and massive manipulation of water flow by either of the two dams in the upper watershed, and serious pollution or related problems by new industrial plants and developments along the river must be minimized; (6) there is no indication at this time of the need for reduction in numbers of white perch by removal netting or chemical eradication, spawn destruction, and other drastic means suggested for overcrowded, landlocked populations in the New England states, or contrariwise, in the event of serious depletion, white perch hatcheries or restocking with fingerlings or adults; and (7) fishermen should be able to increase their utilization of the species through relaxed fishing regulations, increased publicity and education through demonstration netting, news releases of unusual concentrations or migrations, where and how to fish for the species, and the clear explanation of the principles of fish population biology and their practical application.

The prognosis of the white perch fishery is complex and dependent on the nature of catch regulations, biological management, and watershed use and abuse. If a conservative approach continues when the population is not fully exploited, then the number of legal-size fish will remain low, growth rates will be below average or very low,

the bulk of the available fish will be sublegal, and many of these will be lost by natural mortality, or if caught, some will die when returned to the water. In general the species is not efficiently utilized or managed under these conditions, and both the harvest and biology of the species is adversely affected. Continuation of the present methods of management will strengthen the opposition of certain elements among anglers and netters who are interested in liberalized regulations for white perch.

If a liberalized approach is carried out, i.e., relaxation or removal of size limits and any restrictions by gear or area, unless the measures are clearly known to be deleterious to the population, then improvements in the catch and the biology of the species should follow. Such measures should be flexible so that size, creel, and other limits can be adjusted to changes in fishing intensity, growth, and in population size. Any improvements in management should be accompanied by a monitoring program to assess the effects in terms of changes in the (a) average size and age of harvested fish by type of fishing and fishermen; (b) rate of growth and availability of sizes and ages; (c) catch-per-unit-effort and total catch; (d) age and size composition, and numerical strength, of fish on the spawning migrations; and (e) effects of regulations, if possible, on other species. White perch under liberalized management measures should be observed carefully in order to preclude serious problems of availability arising from very low year-class success, sudden mortalities induced by nature or by man, and extensive exploitation. Reduction or removal of size limits will create problems in commercial fishing operations and marketing, and some opposition should be expected from a segment of the netters. The latter will be balanced by proponents of liberalized fishing among sport and commercial fishermen. There is no doubt that many of the unexploited small fish below 8 inches T.L. can be used for home consumption and marketed.

The results of this study show that the white perch in the Patuxent estuary are fairly stable in numbers, possess growth characteristics slightly below average for the species, but are not receiving optimum use. Reduction or removal of size limits provide the only positive measure that will bring about biological improvement and effective utilization of the population. Encouraging and educating certain fishermen to use and remove all white perch above 5 inches, concurrently with a monitoring program, will provide a basis for improved management of the species in the estuary.

Conclusions

(1) The Patuxent River estuary, a tributary of Chesapeake Bay in Maryland, contains an important and homogeneous population of white perch living from its confluence with the Bay for a distance of about 60 miles to tidal fresh water. This species is one of the most important food and game pan-sized fish resident there. The tidewater portion of the river, which was divided into 6 zones from fresh to salt water at the mouth is used variously for spawning, nursery, feeding, and wintering grounds by the species. The fish rarely enter a seventh zone immediately outside the river mouth in Chesapeake Bay.

(2) Scales were used to determine the ages of white perch. The scale-length and body-length relationship resulted in a straight line, and the extrapolated intercept of this line on the body-length axis was 16.3 mm. This artificial value was assumed to be the size at apparent scale formation, and examination of young fish between 9.0 and 28.0 mm confirmed this observation. It was used as a correction factor in back-calculating lengths at various ages.

(3) A comparison of growth histories of male and female white perch calculated by the direct proportion and by the body-scale correction method indicated that error in estimation may be as great as 20 per cent in age group I, decreasing proportionately with an increase in age.

(4) Mean sizes for corresponding ages compare well when the observed were contrasted to the calculated growth rates. Small statistically significant differences occurred between calculated and observed mean lengths of the younger age groups of

both sexes; these were partially attributed to the effects of gear selectivity in which sampling biased for larger fish by commercial nets occurred.

(5) The mean sizes of males is less than that of females at a corresponding age. The growth increments for both sexes were greater the first year than in any other year, decreasing rapidly after age group II. Great variation was encountered in the mean observed weight attained by white perch at each age. Female fish weighed more than male fish at the same age and length.

(6) Many males and almost all females enter the commercial and sport fishery at the legal size of 8 inches total length at age group V. Growth rates of white perch from Maine and Maryland were very similar for the first 10 years, although Maine white perch exceeded the life span of Maryland fish by 6 years. Apparent growth rates of Patuxent River white perch differed somewhat from those studied in Nova Scotia, Massachusetts, Rhode Island, New York, and North Carolina.

(7) An examination of the age and year-class composition of the 1948–1955 collections did not reveal an overwhelming abundance or dominance of a particular year-class, although minor fluctuations were evident. Average differences in growth histories of the year-classes of Patuxent River white perch from 1942-1954 between the various calendar years were not very great, although certain years revealed marked fluctuations.

(8) Various meteorological and hydrographical factors and an index of population density were correlated with the first-year growth of white perch for the 13-year span, 1942–1954. A positive correlation exists between the latter and (a) growth time in days between water temperatures at 10° and 15° C and (b) solar radiation in light energy from February to June. A negative correlation exists between first-year growth and (a) rainfall from February to May and (b) population density as reflected by the commercial haul seine catch in the Patuxent River.

(9) The correlation of first year growth and the index of population density suggests that when white perch populations are large in numbers the individuals from which they arise are usually small-sized. When the populations are small in numbers, the individuals composing them on the average are large-sized. The relationship suggests that competition for food supply among fish populations of different densities may be an important factor.

(10) Of 3024 white perch tagged with Petersen disks, consisting of 1117 females, 1448 males, and 489 fish of unknown sex, 324 (10.7%) were subsequently recovered by commercial netters (92.3%) and some sport fishermen (7.7%). The population is essentially an isolated and self-contained one, with the high salinity at the confluence of the estuary and Chesapeake Bay possibly representing an effective physiological barrier against any but a minor degree of emigration. Only three recoveries were made outside the Patuxent estuary. Those tagged in Chesapeake Bay outside the river were not considered part of the Patuxent population; none entered the river. They migrated far up the bay.

(11) There were seasonal differences in movements. Spring-tagged fish traveled in an upstream direction before, and downstream after, spawning. Summer movements were essentially local and random, while fall movements were downstream toward deep water. During winter the fish remained in deep areas and did not migrate until spring. The freedom interval had little influence on the distance migrated. There did not appear to be sexual differences in mean distances traveled and time free. The recoveries of tagged fish were not confined to a particular size range, nor were they limited to legal-sized fish.

(12) Meristic studies of samples of 600 white perch from within and outside the Patuxent estuary generally support the homogeneity of the Patuxent population based on tagging studies conducted in the river, and indicate the occurrence of a number of different subpopulations in Chesapeake Bay and its tributaries. Morphologically, the Patuxent River white perch are related to the Potomac River population. It is concluded tentatively that, since

there is a lack of evidence of interbreeding between these populations, the two populations possibly had the same genetical origin and ecologically are affected by their environment in a similar manner.

(13) Statistically significant differences exist between sample means of meristic counts for white perch from different tributaries and areas within the Chesapeake Bay area, indicating that probably each tributary has its own population, and that even within the Chesapeake Bay, discrete local populations exist. The level of differentiation among them as indicated by these measurements, however, is low. Although meristic numbers are genetically fixed within certain narrow limits, it is emphasized that environmental effects are important, may vary from year to year within a population, and may account for the phenotypes observed.

(14) White perch are semi-anadromous, estuarine fish that undertake relatively large-scale migrations within the estuary for spawning purposes. Female white perch are oviparous and fertilization is external. No external characteristics have been found to differentiate the two sexes, except during the spawning season. From April to May spawning takes place in tidal fresh and slightly brackish water when water temperatures are between 10° and 15° C. White perch spawn once a year, but ovulation is apparently spread over a period of a week or more.

(15) Males mature at a smaller size and earlier age than females. The standard length at which 50% of the males are sexually mature is 100.3 mm and for females 105.5 mm. All males in age group II and older, and a small proportion of females of age group II and III, were sexually mature. Among females in these age groups, sexual maturity seemed to be related to size rather than age. All females above age group IV were sexually mature.

(16) Males predominated over females in numbers on the spawning grounds, while females exceeded males in the lower estuary during the spawning period. This unbalanced sex ratio on the spawning grounds is partly attributed to the large numerical occurrence of young males and the lack of immature females from age groups II and III. Gear selection also accounts for the loss of more large females than males before they reach spawning areas.

(17) Mortality rates calculated from the log plot of age frequencies in the form of a catch curve for males, females and sexes combined, revealed that the unweighted annual probability of dying (=annual mortality rate) for males (50%) was less than for females (56%). Survival among the exploited white perch populations is relatively good when compared to values obtained from unexploited and exploited populations of other fish species. The analysis also indicates that the Patuxent white perch population is not overfished.

(18) The probability of dying varies somewhat from age group to age group, although the value for age group VI is the closest approximation to the calculated mortality rate for all above age group IV. The probability of dying computed from data on white perch in Maine compared favorably with the Maryland data, although the catch curve for Maine is shifted 6 years to the right on the age scale. The apparent probability of dying for fish under age group V subject to death largely by natural causes is similar to that for fish older than this group subject to death due to natural and fishing mortality by man.

(19) A life table was provisionally constructed for adult white perch beginning at age group IV based on the age at death method. The mean life expectancy for a cohort was slightly more than 1½ years, and this value compares favorably with low mean values calculated for certain birds. This indicates that generally the chances of survival among white perch at any age is not very great. A survivorship curve resulted in a straight diagonal line, indicating that age specific mortality rates are constant. It is similar to that of the hydra, certain birds, and possibly the snowshoe hare. It was hypothesized that a complete life table for white perch should start with a cohort of eggs or larvae, in which case a J-shaped curve would probably result.

(20) Management of the white perch in

the estuary is related to their population homogeneity and restricted distribution, considerable small size and early age at spawning, slightly below average growth rate, low proportion of available keeper-sized fish to fishermen, and the apparent moderate exploitation. Reduction or removal of the 8-inch minimum legal size is the only positive management measure that will bring about the effective use of the population, an increase in the rate of growth and average length of individual fish, and possibly improve their catchability. Liberalized management should be accompanied by a concurrent monitoring study to assess the effects of the change.

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Notes and Comments

The Copepod Genus *Acartia* in Chesapeake Bay

ABSTRACT

Chesapeake Bay specimens of *Acartia*, identified by C. B. Wilson as *A. clausii* and *A. longiremis*, were re-examined. All the specimens identified as *A. longiremis* and most of those labelled *A. clausii* were *A. tonsa*. *A. clausii* was present only in two winter samples. The postulated change in the composition of species of *Acartia* in the Bay can no longer be supported, since it arose from Wilson's misidentifications.

In his study of the pelagic copepods of Chesapeake Bay, based upon about 1000 samples collected in 1915–16 and 1920–21, Wilson (1932) reported that two species of *Acartia*, *A. clausii* Giesbrecht and *A. longiremis* (Lilljeborg), were present in nearly every sample and numerically constituted about two-thirds of the entire collection.

Davis (1944), studying samples collected mostly in 1942, found *Acartia tonsa* Dana to be the dominant planktonic copepod in Chesapeake Bay. *A. clausii* was taken only during the winter months and was always less abundant than *A. tonsa*. Davis did not find *A. longiremis*. The discrepancy between his findings and those of Wilson led Davis to postulate "an important ecological evolution in the Chesapeake Bay over the course of only a few years." This supposed change in species dominance is mentioned by Deevey (1948); she points out that it is impossible to tell from Davis' data whether *A. tonsa* had become dominant thruout the year or only seasonally. No evidence for a concomitant change in the physical and chemical properties of the Bay water has been advanced.

A summary of the known distribution of the three species of *Acartia* along the northeast coast of the United States is given below, since this should give us an understanding of and be consistent with their distribution in Chesapeake Bay.

In the Gulf of Maine *A. tonsa* was not found by Bigelow (1926), who states that Cape Cod appears to be the northern boundary of its presence in numbers. *A. clausii* is widespread and abundant, especially in shoal waters. *A. longiremis* is widespread, but never very abundant.

Between Cape Cod and Chesapeake Bay *A. tonsa* and *A. clausii* are abundant in coastal water and in bays, but are seldom found over the continental shelf (Bigelow and Sears, 1939). Both occur at Woods Hole (Fish, 1925), at Tisbury Great Pond, Massachusetts (Deevey, 1948), in Rhode Island waters (Williams, 1906, 1907; personal observations), in Block Island Sound (Deevey, 1952a, 1952b), in Long Island Sound (Conover, 1956; Deevey, 1956), and in Delaware Bay (Deevey, 1960).

In Long Island Sound *A. clausii* is dominant in winter and spring, *A. tonsi* in summer and early fall. Whereas the maximum numbers of *A. clausii* are somewhat greater than those of *A. tonsa* in Long Island Sound (Conover, 1956), the reverse is true in Delaware Bay where *A. tonsa* ranks as the dominant copepod species, *A. clausii* being less important both in numbers and seasonal range (Deevey, 1960). In Block Island Sound, which is more open and more influenced by oceanic water, the numbers of *A. clausii* and *A. tonsa* are much less than in Long Island Sound.

A. longiremis does not inhabit the above bays and sounds, with the exception of Block Island Sound. Bigelow and Sears (1939) found it infrequently over the continental shelf, and in the Delaware Bay region Deevey (1960) found it only from January to May of one year, primarily outside the Bay.

A consistent distribution pattern for the species of *Acartia* along the northeast coast is apparent. *A. tonsa* and *A. clausii* inhabit coastal water and rarely stray over the shelf. *A. clausii*, dominant in the Gulf of Maine, is gradually replaced to the south by the warm-water *A. tonsa*. *A. longiremis* is an inhabitant of shelf water, at least in the southern part of its range, i.e. south of Cape Cod, and does not ordinarily occur in coastal water or in the bays.

If the distribution in Chesapeake Bay fits this pattern, we can expect to find *A. tonsa* dominant most of the year, *A. clausii* present to a limited extent during the winter months, and *A. longiremis* absent. Davis (1944) found precisely this distribution, in contrast to Wilson's (1932) findings. Because of the discrepancy in Wilson's results and the lack of evidence for any drastic change in the properties of the bay water, I have reexamined the Chesapeake Bay specimens of *Acartia* in the U.S. National Museum identified by Wilson in order to ascertain whether his determinations were correct. Wilson deposited five lots identified as *A. clausii* and five identified as *A. longiremis* in the Museum. All the specimens labelled *A. longiremis* proved to be *A. tonsa*. The samples identified as *A. clausii* likewise contained only *A. tonsa*, with the exception of two samples collected in December and January; the latter contained both *A. tonsa* and *A. clausii*. Samples collected in August, October, and November contained only *A. tonsa*.

It is evident, therefore, that the species composition of the genus *Acartia* in Chesapeake Bay has not changed drastically, contrary to Davis' suggestion. Two species, *A. clausii* and *A. tonsa*,

occur in the Bay. Their seasonal distribution remains to be elucidated, but it appears that *A. tonsa* is the dominant species during most of the year, whereas *A. clausii* is less important than in the cooler waters of Long Island Sound and perhaps less than in Delaware Bay. There is no evidence that *A. longiremis* occurs in Chesapeake Bay, and it is not ordinarily found in coastal water south of Cape Cod.

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Iron in Chesapeake Bay Waters[1]

ABSTRACT

Total iron determinations in Chesapeake Bay off the Patuxent River mouth, Maryland, indicate that surface water layers contain relatively low iron concentrations typical of upper bay areas while bottom layer concentrations reflect high levels found within the range of Atlantic coastal waters. These results are related to the sharp two-layered stratification of Chesapeake Bay in midsummer.

The Chesapeake Bay typically develops a sharp two-layered stratification in midsummer. The bottom waters show higher salinities, usually a lower temperature, lower pH, and oxygen deficiency, compared with the top water layer. Occasionally the oxygen-poor bottom waters smell of hydrogen sulfide when first sampled. Since iron is vital in the nutrition of the anaerobic sulfate-reducing bacteria of the genus *Desulfovibrio*, iron determinations were made from the water column during this summer stratification.

A Kemmerer sampler was used to take water samples from the water column in the main channel of the Chesapeake Bay, off the confluence of the Patuxent River, near the red nun buoy "16 E," (37° 21′ 37″ N., 75° 18′ 47″ W., U.S.C. & G.S. Chart #553). The water depth at the sampling station is approximately 130 feet. Sample was taken on 26 July 1960, 1500 EDST, ebb tide, sky clear, water rough, wind SE 15–20 knots.

Total iron was determined with the method described by Lewis and Goldberg (1954), using bathophenanthroline. Results for iron determinations are the mean of three replications of each sample. Ancillary data taken included salinity (hydrometer method), temperature (electronic thermistor casting thermometer), dissolved oxygen (Winkler method), pH (cresol red indicator), and light penetration with a Secchi disc. The Secchi disc reading was 6 feet. The distribution of these environmental variables is shown in Fig. 1.

A sharp difference between the top and bottom water layers can be seen on this graph. The strata seem to be delineated between the 20 and 40 foot level.

Iron analyses in natural waters, both fresh water and marine, show much variation. This can be seen in the replicates in Table 1. Martin (1956) shows iron values in some freshwater tributaries of the upper Chesapeake Bay ranging from 0.01 to 0.10 mg/l. In a study of pollution in Baltimore Harbor, Garland (1952) found up to 140 mg/l iron in certain areas of Baltimore Harbor, and a median

[1] Contribution No. 188, Natural Resources Institute of the University of Maryland, Chesapeake Biological Laboratory, Solomons, Maryland.

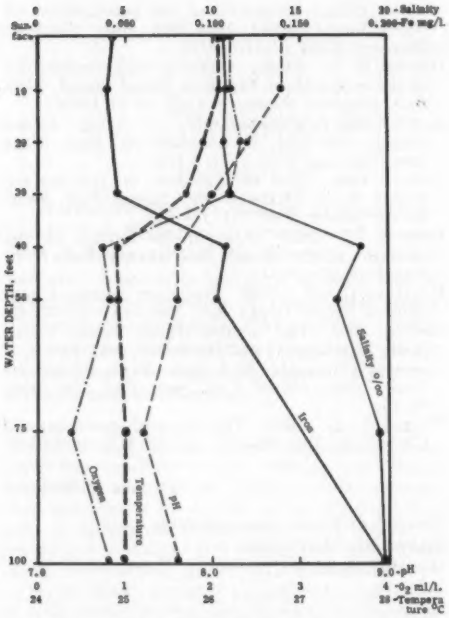

Fig. 1.—Distribution of total iron and other variables with depth in Chesapeake Bay, off the Patuxent River, Maryland.

range of 0.29 to 1.40 mg/l in Bay waters just outside the harbor. He concluded, however, that "There is no indication that waste disposal, as normally practiced in the area, has any significant effect on water quality in Chesapeake Bay outside Baltimore Harbor."

Lewis and Goldberg (1954) in a compilation of the literature of iron values in sea water, indicate that 19 to 91 mg/l Fe have been found along the coasts of North America. Their determinations of deep North Pacific waters indicate 8 micrograms/l (0.008 mg/l) of iron, with higher, but more variable, concentrations in surface waters.

Schaefer and Bishop (1958), in a study of the distribution of particulate iron (that retained on a molecular filter) in the Gulf of Panama, found a tributary river to contain 692 to 863 microgm/l (0.692 to 0.863 mg/l), the surface waters in the Gulf to average 115 microgm/l (0.115 mg/l), and lower values (0.062 mg/l) at 30 meters.

The iron determinations reported in this paper are of total iron, i.e., no attempt was made to discriminate "particulate" and "soluble" iron by filtration. In general, the surface water layers seem to reflect the relatively low iron concentrations of the upper tributary rivers (excluding Baltimore Harbor), and the bottom layer concentrations of iron fall within the range of Atlantic Coastal waters.

TABLE 1.—Iron in a Chesapeake Bay Water Column.

Sample depth	Iron, mg/l
Surface	0.045
	0.043
	0.040
	Mean = 0.043
10 ft.	0.045
	0.031
	0.043
	Mean = 0.040
30 ft.	0.044
	0.044
	0.048
	Mean = 0.045
40 ft.	0.098
	0.074
	0.154
	Mean = 0.108
50 ft.	0.117
	0.089
	0.104
	Mean = 0.103
100 ft.	0.192
	0.213
	0.225
	0.224
	0.172
	Mean = 0.205

Iron is implicated in the growth of phytoplankton, especially diatoms, in the nutrition of *Desulfovibrio* and in the chemical depletion of oxygen by oxidation of ferrous to ferric iron.

These data would indicate that iron would not be limiting in the biological systems considered, but the role of iron in causing or contributing to oxygen depletion must await more comprehensive determinations of iron in Chesapeake Bay waters in both ferrous and ferric valence states.

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Further Returns of Striped Bass, *Roccus saxatilis*, Tagged from Deep Water During Winter in Chesapeake Bay, Maryland[1]

ABSTRACT

Striped bass tagged during winter (N = 104) from depths of 60 to 80 feet were recaptured (N = 14, 13 per cent) in two general areas, the upper Chesapeake Bay and the Potomac River, during the following 10 months. They were tagged in January, 1959 from drift gillnets that exploited overwintering aggregations in waters just above freezing. About half of the fish exhibited over-inflated swimbladders due to rapid ascent and pressure decreases, but the remainder showed no such evidence externally. Recaptured fish were represented about equally by these two general groups. The study corroborated previous studies that striped bass can be tagged and released from deep water of Chesapeake Bay, be subjected to winter hazards in tidewater, and still be recaptured in sufficient numbers to provide meaningful data for longterm investigations.

Introduction:—The purpose of this tagging study of striped bass, *Roccus saxatilis* (Walbaum), was threefold: (1) to augment fragmentary marking studies of fish overwintering in deep water; (2) to check further into survival from deep water of rapidly-raised fish which were characterized by over-distended swimbladders; and (3) to determine rate, time, and dispersal routes of fish taken from these areas of concentration. Since certain phases of long-range investigations on this species may be directed toward the winter marking studies, data of all types for this period is of importance in the design of experiments. Striped bass overwinter on the bottom slopes and in the channel of the open Chesapeake Bay. While each river apparently has a small number of overwintering fish in the lower reaches, the bulk of Maryland striped bass are found in aggregations in the open bay from Worton Point and Aberdeen to the area between the Patuxent and Potomac River mouths. This conclusion is based on fishing trips taken with netters, an examination of winter catch records, interviews with drift gillnet fishermen, and experimental trawling surveys cited herein.

Methods and materials:—All fish were taken by a licensed commercial drift gillnetter (fishing principally with 3¾″ to 4½″ stretch mesh) on January 8, 1959 in the open Chesapeake Bay north of Cove Point, Calvert County, to Punch Island Creek and the area below the mouth of the Little Choptank River, Dorchester County. The depths ranged from 60 to 80 feet, although areas 90 feet deep yielded some fish. The nets were drifted during a tidal cycle for periods of 2 to 4 hours (Fig. 1C), then lifted at a rate of about 20 to 30 feet per minute. Fish were rapidly removed by fishermen from the mesh and usually handed to the taggers. Sometimes the nets were lifted more rapidly because of heavy seas, changing wind, and tides. All fish were brought up alive and moved with great vigor, but those left on the deck more than 2 or 3 minutes gradually froze.

The fish were tagged with red plastic Petersen disks in the same manner described by Mansueti (1956:1–2; 1961:12). The tags were stamped with a number, an address to which the tags should be returned, and a statement of a reward, which was $1.00. Appreciation is extended to the U. S. Bureau of Commerical Fisheries, Beaufort, North Carolina, for supplying the tags and paying the rewards. Fishermen were informed of the tagging operation by personal contact and by some newspaper publicity. Data on length, weight, sex, location and depth of capture, and swimbladder inflation were taken on each fish as well as other relevant data on behavior as outlined by Mansueti (1956:3). A length frequency distribution of the tagged and recaptured fish is given in Fig. 1B.

Biology of the fish:—The mesh size of the gillnets restricted the length range of the available fish to those between 11 and 17 inches F.L. (Fig. 1B), with the exception of a specimen 30.1 inch F.L. that weighed 16 pounds, 8 ounces. The latter fish was not recaptured. All other fish comprised age groups II and III, based on scale examination of a sample of these fish. Of the 104 fish, 36 were sexually mature, ripe-running males. Fig. 1B also shows that the lengths of the recaptured fish, at tagging, were fairly representative of the marked sample.

[1] Contribution No. 189, Natural Resources Institute of the University of Maryland, Chesapeake Biological Laboratory, Solomons, Maryland.

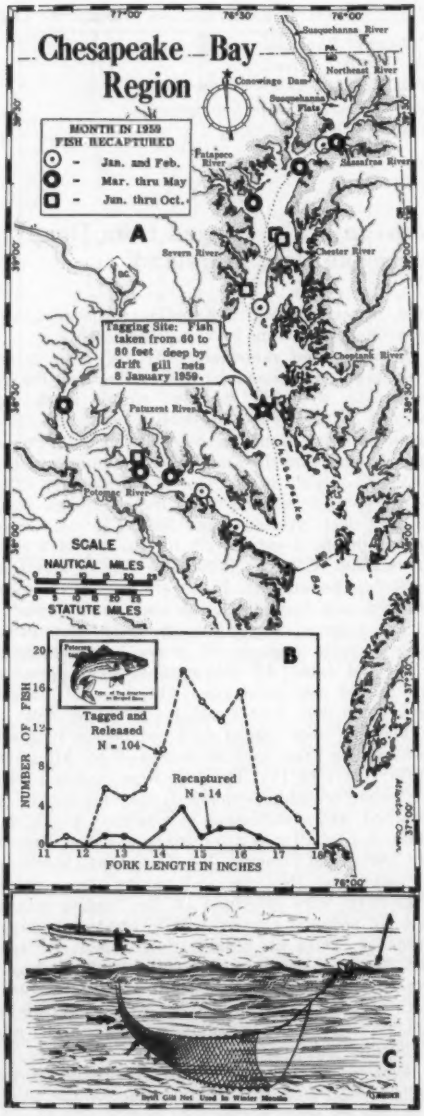

Fig. 1.—Locations of recaptures of striped bass, *Roccus saxatilis*, tagged during winter from drift gillnets, with: (A) seasonal recaptures restricted entirely to the Maryland part of the Chesapeake Bay; (B) length frequency distribution at tagging of released and recaptured fish; and (C) general appearance of drift gillnets operating in deep water during winter.

Tag returns:—A total of 14 tags (13.4 per cent) were returned within 10 months as follows: January—2; February—1; March—4; April—3; May—1; August—2; and October—1. Recoveries were made as follows: stake gillnets—5; anchor gillnets—1; gillnets—2; pound nets—1; haul seines—1; and hook and line—4.

Dispersal pattern:—Fig. 1A shows the locations of recapture in gross relation to time. In general the recoveries were concentrated in two regions: (a) upper Chesapeake Bay (8 returns); and (b) the Potomac River (6 returns), and all were confined to Maryland as in previous studies cited below. These results would suggest a conditioned predilection by the fish to enter areas that probably represent spawning and feeding locations. Thus, the dispersal cannot be interpreted as random movements as was suggested by Mansueti (1956:6) in a similar study. He reported recaptures that seemed to have dispersed radially from the same tagging site as the fish reported herein. Returns of fish tagged in January, 1958 (Mansueti, 1961:29) were entirely from the Maryland span of the open Chesapeake Bay; none came from the tributaries. There was no evident relationship between the freedom interval in days after tagging and distance traveled in miles, a conclusion that is apparent in Fig. 1A.

The returns, divided into the Potomac River and upper Chesapeake Bay recaptures, suggest that the overwintering aggregations may represent two or more stocks or subpopulations, and that after initial movements in late February and early March, there was a segregation of fishes according to their affinity for certain tributaries. Since any females in the length range given in Fig. 1B are virtually all immature, their choice is not conditioned by previous spawning migrations. Furthermore, it is not known for certain whether these immature females migrate as far upstream to the spawning area as do the small sexually mature males. Mansueti (1956:6) suggested the possibility that striped bass may return to rivers to which they have been conditioned, but that available data and returns were too fragmentary for a stronger statement. The 1959 data has not improved our knowledge in this direction. The 1954 recoveries came from within the Choptank and Wicomico Rivers and close to other tributaries during the spring migration, while none of the 1959 group entered these tributaries during the same season. The available evidence suggests that the open Chesapeake Bay may serve as an important, but not exclusive, overwintering area for a large part of the fish present in the whole system. Also, the choice of tributary does not seem random, but a clear explanation of how it is made and whether it is due to previous residence is not possible as yet.

Bottom distribution of wintering striped bass:—Observations were made on the nature of the bottom and slopes of the bay where the gillnets were drifted in relation to depths and loca-

TABLE 1. Summary of the published results of winter tagging studies with striped bass, *Roccus saxatilis*, from various localities.

Reference	Tagging Site	Date of Tagging	Method & Depth of Capture	Size & Age Groups of Fish	Number Tagged	Number & Per cent Recaptured	Months of Recovery
Clark (1936:275–81)	California, Sacramento—San Joaquin Rivers	Jan., Feb., & Dec. 1932–35	Hook & line; depth unknown	8–20″ F.L.; [age groups I–IV]	48	3 (6%)	Aug. & Sept. 1933
Vladykov and Wallace (1938: 67–86; 1952: 167–74)	Virginia, James R. Newport News	Jan. 1937	Fyke nets; depth unknown	8.1–20.2″ F.L.; [age groups largely II–III]	42	14 (33.4%)	Jan. to Apr. 1937
Calhoun (1952: 393–5)	California; Sacramento—San Joaquin Delta	Jan.–Feb. 1947 & 1951	Gillnets (including drift nets); 8 to 30 feet deep.	25 to 37″ F.L.; [age groups variable]	*ca* 336 in 1947	*ca* 22 (7%)	Jan. to Mar. 1947–8, 1951–2
Mansueti (1956: 4–6)	Maryland Chesapeake Bay, nr. Patuxent R.	Feb. 1954	Drift gillnets; 80 to 120 feet	9.2–15.5″ T.L.; [age groups II–III]	31	11 (35%)	March & April 1954
Mansueti (1959: 3)	Maryland, Potomac R. in mid-estuary	19 Jan. to Feb. 4, 1959	Trawls, 30 to 60 feet in mouth widths; 30 to 100 feet deep.	[8–20″ F.L.; age groups I–IV]	739	167 (23%)	Jan. to Nov. 1959
Chapoton and Sykes (1960:7)	North Carolina, Atlantic Ocean coast	3–10 Dec. 1956 2–23 Dec. 1958	Haul seines; [5 to 20 feet deep?]	21.5–48.8″ F.L.; [age groups IV–XVI.]	79	19 (24%)	Dec. to Sept. 1956 & 1958?
Mansueti (1961: 29)	Maryland, Chesapeake Bay, from Potomac R. to nr. Sassafras R.	8–9 Jan. 1958	Semi-balloon trawl (30 ft. mouth); [20 to 120 feet deep]	5.5–15.5″ F.L.; [age groups 0–II.]	176	14 (8%)	Jan. to Sept. 1958
Massmann and Pacheco (1961: 39–41)	Virginia, York R. in mid-estuary	13–27 Feb. 1957 24–28 Feb. 1958	Semi-balloon, trawl (11 ft.) mouth; [30 to 60 feet deep.]	7.0–34.9″ F.L.; many age groups 8.0–26.9″ F.L.; many age groups	367 1,004	142 (39%) 276 (27%)	Winter thru autumn
Mansueti (this study)	Maryland, Chesapeake Bay, nr. Patuxent R.	8 Jan. 1959	Drift gillnets; 60 to 80 feet deep.	11.0–18.0″ F.L.; [age groups II and III]	104	14 (13%)	Jan. to Oct.

tions of the fish that were snagged in the gear. The gillnets average 8 feet in depth, were approximately 1000 yards long, and were weighted down by cement bags tied to steel rings (Fig. 1C). These were put overboard across the flow of the bay, and marked at each end with a spar buoy and large flotation can. Attempts were made to relate the depths and locations of fish catches in relation to fathometer tracings of the bottom contour. These general observations were made during the tagging trip and other winter periods: (1) striped bass are caught in clusters, which seemed to be random throughout much of the length of the net; (2) the middle two-thirds of the net contained most of the fish, but there was no numerical concentration where the apex would be located; (3) many fish were taken from areas represented by "slopes" on the bay bottom, although some aggregations were taken from "holes;" and (4) temperature variations of few degrees had a marked effect on the depth distribution and geographic dispersal, i.e., warming conditions were accompanied by extensive movements from the holes onto the slopes and into relatively shallow water; while prolonged and abnormally cold conditions reduced movements and concentrated the fish into deep areas.

Swimbladder over-inflation and recovery:— As striped bass were brought aboard, they were examined grossly for over-inflation of the swimbladder. The fishermen cooperated by pulling up the nets more slowly than usual, so that only a few of the fish were abnormally-inflated. None, however, exhibited "oral extrusion" of the internal structure forced by the enlarged swimbladder as recorded by Mansueti (1956:6). About half of the fish were perceptibly over-inflated, while the remainder exhibited no evident inflation. Recaptured fish were represented about equally by these two general groups, thus the overinflated swimbladder apparently does not impede recovery. When the fish were thrown overboard, the latter

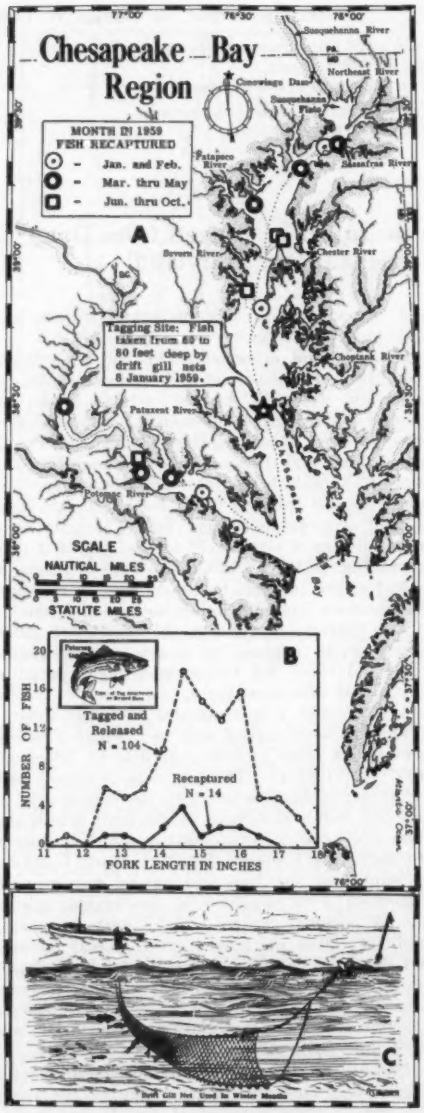

Fig. 1.—Locations of recaptures of striped bass, *Roccus saxatilis*, tagged during winter from drift gillnets, with: (A) seasonal recaptures restricted entirely to the Maryland part of the Chesapeake Bay; (B) length frequency distribution at tagging of released and recaptured fish; and (C) general appearance of drift gillnets operating in deep water during winter.

Tag returns:—A total of 14 tags (13.4 per cent) were returned within 10 months as follows: January—2; February—1; March—4; April—3; May—1; August—2; and October—1. Recoveries were made as follows: stake gillnets—5; anchor gillnets—1; gillnets—2; pound nets—1; haul seines—1; and hook and line—4.

Dispersal pattern:—Fig. 1A shows the locations of recapture in gross relation to time. In general the recoveries were concentrated in two regions: (a) upper Chesapeake Bay (8 returns); and (b) the Potomac River (6 returns), and all were confined to Maryland as in previous studies cited below. These results would suggest a conditioned predilection by the fish to enter areas that probably represent spawning and feeding locations. Thus, the dispersal cannot be interpreted as random movements as was suggested by Mansueti (1956:6) in a similar study. He reported recaptures that seemed to have dispersed radially from the same tagging site as the fish reported herein. Returns of fish tagged in January, 1958 (Mansueti, 1961:29) were entirely from the Maryland span of the open Chesapeake Bay; none came from the tributaries. There was no evident relationship between the freedom interval in days after tagging and distance traveled in miles, a conclusion that is apparent in Fig. 1A.

The returns, divided into the Potomac River and upper Chesapeake Bay recaptures, suggest that the overwintering aggregations may represent two or more stocks or subpopulations, and that after initial movements in late February and early March, there was a segregation of fishes according to their affinity for certain tributaries. Since any females in the length range given in Fig. 1B are virtually all immature, their choice is not conditioned by previous spawning migrations. Furthermore, it is not known for certain whether these immature females migrate as far upstream to the spawning area as do the small sexually mature males. Mansueti (1956:6) suggested the possibility that striped bass may return to rivers to which they have been conditioned, but that available data and returns were too fragmentary for a stronger statement. The 1959 data has not improved our knowledge in this direction. The 1954 recoveries came from within the Choptank and Wicomico Rivers and close to other tributaries during the spring migration, while none of the 1959 group entered these tributaries during the same season. The available evidence suggests that the open Chesapeake Bay may serve as an important, but not exclusive, overwintering area for a large part of the fish present in the whole system. Also, the choice of tributary does not seem random, but a clear explanation of how it is made and whether it is due to previous residence is not possible as yet.

Bottom distribution of wintering striped bass:—Observations were made on the nature of the bottom and slopes of the bay where the gillnets were drifted in relation to depths and loca-

TABLE 1. Summary of the published results of winter tagging studies with striped bass, *Roccus saxatilis*, from various localities.

Reference	Tagging Site	Date of Tagging	Method & Depth of Capture	Size & Age Groups of Fish	Number Tagged	Number & Per cent Recaptured	Months of Recovery
Clark (1936:275–81)	California, Sacramento—San Joaquin Rivers	Jan., Feb., & Dec. 1932–35	Hook & line; depth unknown	8–20″ F.L.; [age groups I–IV]	48	3 (6%)	Aug. & Sept. 1933
Vladykov and Wallace (1938: 67–86; 1952: 167–74)	Virginia, James R. Newport News	Jan. 1937	Fyke nets; depth unknown	8.1–20.2″ F.L.; [age groups largely II–III]	42	14 (33.4%)	Jan. to Apr. 1937
Calhoun (1952: 393–5)	California; Sacramento—San Joaquin Delta	Jan.–Feb. 1947 & 1951	Gillnets (including drift nets); 8 to 30 feet deep.	25 to 37″ F.L.; [age groups variable]	*ca* 336 in 1947	*ca* 22 (7%)	Jan. to Mar. 1947–8, 1951–2
Mansueti (1956: 4–6)	Maryland Chesapeake Bay, nr. Patuxent R.	Feb. 1954	Drift gillnets; 80 to 120 feet	9.2–15.5″ T.L.; [age groups II–III]	31	11 (35%)	March & April 1954
Mansueti (1959: 3)	Maryland, Potomac R. in mid-estuary	19 Jan. to Feb. 4, 1959	Trawls, 30 to 60 feet in mouth widths; 30 to 100 feet deep.	[8–20″ F.L.; age groups I–IV]	739	167 (23%)	Jan. to Nov. 1959
Chapoton and Sykes (1960:7)	North Carolina, Atlantic Ocean coast	3–10 Dec. 1956 2–23 Dec. 1958	Haul seines; [5 to 20 feet deep?]	21.5–48.8″ F.L.; [age groups IV–XVI.]	79	19 (24%)	Dec. to Sept. 1956 & 1958?
Mansueti (1961: 29)	Maryland, Chesapeake Bay, from Potomac R. to nr. Sassafras R.	8–9 Jan. 1958	Semi-balloon trawl (30 ft. mouth); [20 to 120 feet deep]	5.5–15.5″ F.L.; [age groups 0–II.]	176	14 (8%)	Jan. to Sept. 1958
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group sounded immediately, disappearing in a few seconds. Those that were inflated remained near the surface for longer periods, some pirouetting before diving below. Others tried to swim down but would bob up to the surface belly up. Less than 10 per cent floated for more than five minutes. None of these were recaptured, hence their fate is not known. Some of these fish were attacked by herring gulls that followed the boats, but all the fish were too large to be picked up by the birds. Other observations of the type cited by Mansueti (1956:3) were made. In general, the vicissitudes of tagging, herring gulls, turbulent water conditions, very low temperatures, etc., were formidable, but they were not sufficient to affect seriously the tagging operations.

Mansueti (1956:6–8) has reviewed in detail the problem of physiological recovery of physoclist fishes with over-inflated swimbladders due to rapid ascent and pressure decreases in winter. In general, these features were pertinent: (1) when striped bass, which are in hydrostatic equilibrium at a depth of 60–80 feet and under a total pressure of about 3 to 3½ atmospheres, are brought up too rapidly, the decrease in pressure results in expansion of the swimbladder, the volume of the fish as a whole increases, and its density decreases; (2) the fish attempt to maintain their station at various levels above the plane of equilibrium by rapid fin movements which promotes resorption of excess swimbladder gases until the density has been restored to that of the environment; (3) from a practical point of view, since the solubility of all gases increases with a decrease in temperature, it is possible that a large portion of the excess gas is resorbed immediately under winter conditions but the rest is assimilated more slowly; and (4) the fair number of tag recaptures indicates that fish apparently respond to conditions suggested above and that tagging of fish from deep water is of practical value.

Table 1 summarizes various tagging studies conducted with striped bass during winter and further amplifies the last point made above. A wide variety of gear have been employed successfully in winter, and although percentage of recaptures have ranged widely, the differences are no greater than percentage recaptures summarized from 15 tagging studies on striped bass conducted during other seasons on both coasts listed by Mansueti (1956:7).

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